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VOL.
28
194

STOCKHOLM. ALB. BONNIERS BOKTRYCKERI 1947

INNEHÅLL

ARTUR HANSSON: The Physiology of Reproduction in Mink (Mustela vison, Schreb.) with Special Reference to Delayed Implantation 1

A. P. BYSTROW: Hydrophilous and Xerophilous Labyrinthodonts 137

G. H. ROUX: The Cranial Development of Certain Ethiopian "Insectivores" and Its Bearing on the Mutual Affinities of the Group 165

TORSTEN PEHRSON: Some New Interpretations of the Skull in Polypterus 399

OL.
28
947

SOME NEW INTERPRETATIONS OF THE SKULL IN POLYPTERUS

BY

TORSTEN PEHRSON

(With 28 figures in the text.)

VOL
28
194

CONTENTS.

Introduction 400

Notes on the Chondrocranium 401

Cartilage Bones 404
- Sphenoid 404
- Occipital 404
- Autosphenotic 404
- Ectethmoid 405
- Opisthotic 405
- Prootic 405
- Mento-mandibular 405
- Articular 405
- Hyomandibular and Accessory Hyomandibular 406

The Sensory Line System 407

The Sensory Canal Pattern in Polypterus, Holosteans and Palaeoniscids 413

Development of Dermal Bones 425
- Nasal 426
- Frontal 430
- Rostral 431
- "Premaxillary" and Antorbitals 431
- Lacrimal 433
- "Maxillary" and Infraorbitals 434
- Quadrato-jugal 436
- Postorbital 438
- Dermosphenotic 438
- Intertemporo-supratemporo-parietal 438
- Extrascapulars 441
- Suprascapulars 442
- Supracleithral 443
- Dentary-splenial 443
- Angular-splenial 444
- Coronoids and prearticular 444
- Preopercular 445
- Vomer 448

Acta Zoologica 1947. Bd. XXVIII.

Dermopalatine, Ecto- and Entopterygoid 448
Metapterygoid 448
Parasphenoid 449
Summary 449
Bibliography 451
Key to Text-figures 454

VOL.
28
947

VOL
28
194

THE PHYSIOLOGY OF REPRODUCTION IN MINK (MUSTELA VISON, SCHREB.) WITH SPECIAL REFERENCE TO DELAYED IMPLANTATION

BY

ARTUR HANSSON

(Institute of Animal Breeding, Royal Agricultural College, Sweden.)

VOL.
28
947

PREFACE.

The present treatise on the physiology of reproduction in mink, is the result of investigations carried out during the years 1939—1946. When the work was begun, the main object was to endeavour to elucidate the causes of the great variations in the length of gestation. However, it soon proved that to do this satisfactorily would call for investigations into the course of reproduction in its entirety. The work thus reached dimensions that had not been anticipated from the beginning. Although it has by no means been possible to solve all the far-reaching problems involved, it is my hope that, on the whole, the work will have added to the knowledge of reproduction in the mink and also have contributed to throwing light on some of the general problems of mammalian reproduction.

The investigations have been greatly facilitated by Professor IVAR JOHANSSON, Director of the Institute of Animal Breeding of the Royal Agricultural College, Sweden. Professor JOHANSSON introduced me to the subject and placed equipment and premises at my disposal; by taking part in innumerable discussions on the subject, and by envincing a never-failing personal interest he has rendered me inestimable service. Professor ARON WESTERLUND, Director of the Institute of Animal Physiology at the same College has also promoted my work by placing his time and great wealth of knowledge at my disposal. For their great generosity I would express my gratitude.

The writer has had the inestimable privilege of discussing with the late Professor ERIK AGDUHR, Director of the Histological Institution of the Uni-

versity of Uppsala, the planning of the histological work, and of discussing with Professor AXEL WESTMAN, Director of the Gyneacological Institution of the Caroline Hospital, Stockholm, some of the endocrinological problems, and with Professor GERT BONNIER, Director of the Animal Breeding Institute, Wiad, Eldtomta, some statistical problems. For these privileges I proffer my respectful thanks.

In carrying out the work I have had several assistants. I would express my appreciation and gratitude especially to Mrs. ANNA LISA APELGREN for her extremely conscientious histological work, and to the agriculturists RUNE APELGREN, ALLAN FRÖLICH and GÖRAN NORBLAD, and to the veterinarian IVAR DYRENDAHL, for god cooperation in the experimental investigations, and to Mr. ALF BACKHOFF for his painstaking care of the experimental animals.

I am also indebted to Mr. S. J. CHARLESTON, Reader in English at the University of Stockholm, for the devoted work he has expended on the translation of the Swedish manuscript into English.

I would further express by unreserved thanks to the Swedish Fur Breeders' Association and especially to the members Messrs CLARENCE HAMMAR and STIG SCHOLANDER for the comprehensive animal material and breeding records which were placed at my disposal and made the work possible.

A. B. Leo, Hälsingborg, and A. B. Pharmacia, Stockholm, placed all the hormones used for the endocrinological investigations at my disposal free of charge. For this great kindness I wish to express my unreserved thanks.

Further, I would express my respectful thanks to the Royal Swedish Academy of Agriculture and to the Swedish Fur Breeders' Association for financial support of the investigations.

VOL
28
194

THE PHYSIOLOGY OF REPRODUCTION IN MINK

CONTENTS

Introduction 4
Earlier investigations within the genus Mustela 5
Mink, Mustela vison, SCHREB. 5
Weasel, „ frenata, cicognani et nivalis 7
Stoat, „ erminea, L. 8
Ferret, „ putorius furo, L. 8
Present investigations 10
I. Material 11
II. Methods 12
III. Analysis of breeding data 13
A. Material 13
B. Mating season 15
C. „ habits 17
D. Season of parturition 20
E. Length of gestation 21
IV. General anatomical survey 27
A. Arrangement of the female sex organs 27
B. Ovary 29
C. Tuba uterina 31
D. Uterus 32
E. Placenta 33
V. Ovulation 35
A. Follicular development 35
B. Influence of mating on ovulation 41
C. „ „ re-mating „ „ 46
D. Factors controlling the number of rupturing follicles 49
VI. Variations in the rate of embryonic development 52
VII. Delayed implantation 64
A. Occurrence of delayed implantation 65
B. Causes of delayed implantation according to earlier investigations 67
C. External factors in delayed implantation in mink 73
1. Temperature 73
2. Light 75
a. Irradiation during anestrus 76
b. „ before and after mating 79
D. Histological changes in the female sex organs correlated with the delayed implantation 80
1. Ovary 80
a. Development of the corpora lutea 80
b. Size of the ovary during the sexual cycle 85
2. Tuba uterina 88
3. Uterus 91
4. Vaginal contents 94
E. Internal factors in delayed implantation 100
1. Administration of progesterone with and without simultaneous administration of small amounts of estrogen to mated, normal and ovariectomized females 101
2. Administration of estrogen to normal mated females 105
3. Administration of gonadotropic substances of urine (PU) and blood serum (PMS) to normal mated females 106
F. Discussions 107
VIII. Factors affecting fertility 113
A. Correlation between the number of ovulated and implanted eggs and the number of cubs born 113
B. Breed, age, date of mating, length of gestation and genetic factors . . . 115
C. System of mating 118
Summary 122
References 126

VOL. 28 1947

INTRODUCTION.

The mink, Mustela vison, SCHREB., which belongs to the genus Mustela within the family Mustelidae, is found in the wild state chiefly in northern North America. According to TUFFORD (1930 a) about twenty geographical breeds can be distinguished there. Owing to the valuable fur of the mink and to the relative ease with which the animal can be held in captivity, it has been bred methodically in Canada since the beginning of this century. During the 1920's breeding stocks were exported to several countries in Europe, including Sweden, in which country mink breeding spread so rapidly that, according to the official statistics, at the time of the outbreak of the war in 1939, there were 107,232 animals, of which 32,624 were characterized as breeding stock.

Of the large number of different wild breeds only a few have been of any importance for the production of the farm bred mink. As KING (1942) pointed out, at the present time only two main breeds can be distinguished, viz. the Alaska or Yukon mink and the Quebec or Eastern mink. The former is larger, darker in colour, has a sexual season which begins later, and is also somewhat more prolific than the Quebec mink.

VOL
28
194

It soon proved from the breeding of mink in captivity that the reproduction of the animal has certain remarkable features, chiefly in respect of the mating conditions and the length of gestation. During the period of about one month that the mating season lasts, the females allow several copulations, without any regular estrous interval. The length of gestation shows very great variations, which is unparalleled among other domesticated animals. There seemed to be no satisfactory explanation, based on scientific research, of these pecularities. Therefore during the year 1939 statistical and experimental investigations were begun, in an endeavour to elucidate these pecularities. It soon proved, however, that it was not possible, with any prospects of success, to isolate the ovulation and gestation problems from those of the other phases of reproduction. From the year 1940 the work was therefore directed on the study of the whole course of reproduction. Owing to the fact that the mink has only a relatively short annual sexual season, these investigations have naturally extended over a very long period, as appears from the fact that not until 1946 had they been carried so far that the writer found it advisable to publish the results in their entirety. As in certain cases the investigations led to results of importance for the practical breeding of mink, it was considered urgently desirable to bring them to the notice of mink breeders. This was done in the form of preliminary communications (HANSSON 1940, 1942, 1943, 1944).

On account of the comprehensiveness of the subject, the introductory discussion of the literature is confined to investigations carried out on the mink and other species within the genus Mustela.

EARLIER INVESTIGATIONS WITHIN THE GENUS MUSTELA.

As some other species within the genus Mustela exhibit certain peculiar reproduction features in common with the mink, this survey comprises all the species that have been studied. In an endeavour to render the presentation clearer, each species has been dealt with separately, special importance being attached to the reproduction of the mink.

MINK, MUSTELA VISON, SCHREB.

The reproduction conditions of the mink in the wild state are not fully known. From observations made by American and Canadian trappers, it has, however, been possible to obtain a general picture, even though, quite obviously, this is none too reliable. According to unanimous statements by TUFFORD (1930 b), KELLER (1937) and HOGDSON (1937), in the wild state the mink lives a typical hermit life. The male and female meet only during the mating season, which falls in February—March. The typical cooing sound which is often heard during this period, is considered to be a means of facilitating the meeting of the two sexes. As soon as copulation has taken place, and the female becomes pregnant, the male usually deserts her. The female searches for a burrow, preferably near a water-course, where she arranges her nest and brings forth her young, of which she is said to take excellent care. At the age of about two months the cubs have developed so far that they can fend for themselves, and therefore family life generally comes to an end.

When methodical breeding with captured mink was begun, interest was stimulated, and the possibilities of gaining a knowledge of the reproduction of mink increased. This increased interest has shown itself chiefly in several popular articles on the mating season and the length of gestation of the mink.

Analysis of breeding data have shown (JOHANSSON 1940) that the mating season of the Quebec mink is generally the month of March, while that of the Alaska mink occurs about a week later. During the mating season the female as a rule allows several copulations, with very varying intervals between them. JOHANSSON found that generally there was a tendency for the second copulation to take place, either one or two days after the first one, or after an interval of 8 days. This tendency was interpreted by ENDERS (1940) to mean that the female's follicles generally grow in waves at intervals of 8 days. As a result of studies of the vaginal secretion, ENDERS also considered that he could prove cyclic changes which confirmed this theory of alternating growth of follicles, which has been thought to show that the female mink has several estrous cycles during one and the same mating season.

In practical mink breeding it has been found that the length of mating is very varied. KELLER (1937) states that short copulations are particularly usual during the beginning of the breeding season, owing to lack of sexual activity in the males at that time. KELLER considers that these short copulations are very uncertain, and therefore recommends fresh matings in such cases. On the other hand he considers that, during the end of the mating season, the copulations are often exceptionally long.

The ovulation conditions in mink have been discussed by several workers. KELLER (1937) considers that ovulation may possibly take place at varying intervals after the mating, for if the time between mating and ovulation varies up to 30 days, it would be possible to explain in that way the great variations in the length of gestation. BAHLCKE (1944) advanced a very remarkable ovulation theory, according to which ovulation is spontaneous and only takes place once during the mating season. During ovulation, he thinks, the eggs are not all discharged at the same time, but at certain intervals. The interval between the first and last ovulated egg might be 8 days or more. BAHLCKE considers that such an ovulation mechanism explains a case in which a female gave birth to young at intervals of 8 days. ENDERS (1938, 1939 a, b, 1940, 1941 a, b) is the only worker who has attempted to elucidate the ovulation of the mink by means of experimental investigations. Unfortunately his results are presented in such a popular form that, in several cases, it is difficult to judge of their value. In one case ENDERS found in the tuba of a female which had been mated 52 hours before the autopsy, three unicellular eggs. As they had no corona radiata, ENDERS estimated their age to be about 16 hours. From this it would follow that ovulation took place 36 hours after the copulation. In another case ENDERS ligatured off the tuba of a female after she had mated and found that, nevertheless, she produced one cub. In view of the interval between the mating and ligaturing, ENDERS concluded that the ovulation had taken place 42—52 hours after the copulation. In order to investigate whether the ovulation was dependent on the mating or not, ENDERS isolated a number of females from males during the mating season. In no case did these females ovulate. Thus, as far as can be judged, ENDERS's results seem to indicate that the ovulation of the female mink is dependent on mating.

In practical mink breeding, the experience was gained at an early stage that the length of gestation varied greatly. On the basis of breeding data which they have collected, several research workers have endeavoured to discover the range of the variations and to analyse their causes (PRELL 1930, KELLER 1937, FUNKE 1939, ENDERS 1939 b, 1940, JOHANSSON 1940, APELGREN 1941, BOWNESS 1942, BAHLCKE 1944, PEARSON and ENDERS 1944 and STEVENSON 1945).

KELLER gives 39—72 days as the variation limits of the length of gestation in mink. FUNKE found a variation from 43 to 63 days, JOHANSSON 41—68 days and BOWNESS 39—76 days.

An extremely interesting observation was made by FUNKE (1939), BOWNESS (1942) and PEARSON and ENDERS (1944), cf. HANSSON (1943). They found a tendency towards a shortening of the length of gestation if the mating took place late in the season. No explanation has been found of this phenomenon.

With the guidance of the conditions found in roe-deer (BISCHOFF 1854, RETZIUS 1900 and KEIBEL 1902) and in the badger (FRIES 1880), PRELL (1930) considered that the variation in the length of gestation in mink may be ascribed to a period of rest, "Vortragezeit", in the fertilized egg before implantation. The length of this period of rest is said to vary and to be the direct cause of the great variation in the total length of gestation. As an alternative to this hypothesis, KELLER (1937) advanced the suggestion that the interval between mating and ovulation shows very great variation, or from some hours to 30—35 days. It is then assumed that the sperms have a corresponding length of life in the female genital organ.

OL.
28
947

From this survey it emerges that our knowledge of the reproduction in mink is very fragmentary. We are unacquainted with the anatomy of the sexual organs and the changes in these organs during the sexual cycle. Further, the ovulation conditions are not known, from which it follows that we cannot arrive at any conclusion as to the causes of the great variations in the length of the gestation period.

WEASEL, MUSTELA FRENATA, CICOGNANI ET NIVALIS.

WRIGHT (1942 a), who studied the long-tailed and short-tailed American weasel, Mustela frenata et cicognani, found a variation in the length of gestation, after mating during February—March, of 35—73 days, with an average of 47 days. Though his material certainly comprised only 13 gestations, this fact is of great interest, as it indicates that the length of gestation in weasels, after mating in February—March, shows variations similar to those in mink. WRIGHT states that, on an average, implantation takes place 21 days after mating. In another investigation WRIGHT (1942 b) was also able to prove the occurrence of unimplanted blastulae in the uteri of American weasels mated in June to July and killed during the autumn and winter months. According to this investigation, implantation does not take place until the month of February. This means that, after mating during the summer estrus, the weasel has a greatly delayed implantation, in complete conformity with what is the case with the stoat cf. WATZKA (1940) and DEANESLY (1943).

DEANESLY (1944), however, was unable to prove any delayed implantation in the European weasel, Mustela nivalis. The gestation period for this species was considered to be 6 weeks. Certain signs indicated, too, that ovulation was dependent on mating.

STOAT, MUSTELA ERMINEA, L.

According to WATZKA (1940) and DEANESLY (1943), the stoat has two sexual seasons per year, in March and in June—July. During the estrus in March pregnancy occurs less frequently but in the cases where it does take place the gestation period is about 8—9 weeks, according to WATZKA, and 6 weeks according to DEANESLY. Both state that in that case the corpora lutea develop normally after ovulation. During the summer estrus the majority of the females become pregnant. After ovulation the eggs are fertilized, and cleavage continues during the passage of the eggs to the uterus. After they have arrived there, development is very greatly retarded. No implantation takes place, but the eggs which gradually attain the blastula stage, lie quite free in the horns of the uterus. This so-called "free vesicle stage" (HAMLETT 1935) continues up to the months of February—March when the embryonic development proceeds at a normal rate up to the time of partus in April—May. According to WATZKA, the total length of gestation is 8—9 months in the case of mating during the summer estrus, and according to DEANESLY 9—10 months, thus 240—300 days longer than gestation after mating during the winter estrus.

WATZKA found that, after mating during the summer estrus the corpora lutea did not develop normally, but were small during the free vesicle stage and only attained full development in connection with implantation. On this point DEANESLY was able completely to verify WATZKA's results. These observations indicate that there is a relation probably of an endocrinous nature, between the development of the corpora lutea and the delayed implantation.

A serious objection can be raised against WATZKA's and DEANESLY's investigations. As the animals were killed in the wild state and subsequently examined there is no check as to the time of the mating. There is therefore reason to ask how it was possible to decide whether a female which was found to be pregnant in the months of February—March had mated during the summer or winter estrus. As the results reached by WATZKA and DEANESLY are of extreme interest, it would be desirable to have them verified by investigations in which the mating of the animals was carefully checked.

FERRET, MUSTELA PUTORIUS FURO, L.

The ferret is an animal which has often been employed for investigations on sexual physiology and therefore several specialized works are available. These works have not been included in this general survey but are discussed in connection with the present writer's investigations.

ROBINSON (1918), who made an excellent study of the histology of the ovary in ferrets, was able to prove that oogenesis did not cease with the cessation of

VOL.
28
194

the growth of the ovary. With this the earlier conception that no oogenesis occurred during the adult stage was thus refuted.

MARSHALL (1904) showed that the ferret has a clearly defined sexual season, with a mating season in March—April and partus in May. He found that if the females were mated, ovulation and impregnation took place, and pregnancy followed in the usual course. If the females were not mated, estrus continued up to 6 weeks and no ovulation took place. In view of this, MARSHALL assumed that the ovulation of the ferret was conditioned by the mating. This has subsequently been confirmed by ROBINSON (1918), HAMMOND and MARSHALL (1930) and HAMMOND and WALTON (1934 a, b). The latter closely investigated the question of the interval between mating and ovulation and found it to be about 30 hours. They also studied how long after ovulation the eggs were capable of fertilization. For this purpose a number of females were mated with vasectomized males, and then, at warying intervals from this sterile copulation, they were mated with a fertile male. The first mating led to ovulation, and the eggs were fertilized at the second mating. In table 1 are presented the results of this investigation. If it is assumed that ovulation takes place 30 hours after the sterile mating and that the sperms reach the tuba within 6 hours after the fertile mating, in the majority of cases the eggs are still capable of fertilization 18—24 hours after ovulation. With further increasing age of the ovulated eggs, the capacity for fertilization rapidly declines, and at the age of 42 hours no egg fertilized and developed into a foetus. The eggs of the ferret appear, however, to preserve their capacity for fertilization for a longer period after ovulation than do those of mice and rabbits, cf. LONG (1912), HAMMOND (1934), MYERS, YOUNG and DEMPSEY (1936).

Table 1. *Influence of the interval between sterile and fertile matings on fertility in ferrets, according to Hammond and Walton (1934 a).*

	Interval between sterile and fertile matings in hours				
	18—24	30—36	42—48	54—60	66—72
Number of females	4	4	5	9	9
Number of pregnant females	4	2	4	4	0
Mean size of litter	6.7	6.5	4.2	1.0	0
Mean number of cubs per female	6.7	3.2	3.4	0.4	0

In cases of mating with vasectomized males HAMMOND and MARSHALL (1930) found that pseudopregnancy followed, the duration of which almost corresponded to the normal length of gestation. The latter was very constant for the 25 pregnancies investigated and averaged 42 days, see table 9.

The Russian steppe polecat, Mustela putorius eversmanni, LESS., which is closely allied to the ferret, has been studied in respect of reproduction by

SCHMIDT (1932). He states that the length of gestation is very constant, 36—37 days. He points out as a peculiarity that if the female loses her young immediately after partus, she exhibits estrus again and permits mating. Seven such females had a second litter after a second mating.

This survey of earlier investigations into the reproduction of various species within the genus Mustela shows systematic differences between them. The female mink has one mating period a year, but the length of the gestation period shows great variations. The weasel and the stoat have one mating season in February to March and one in June to July. As regards weasels, the length of the gestation period after mating in February—March shows a variation corresponding to that of the mink, while, as regards the stoat, conditions in this respect are not known. In the case of gestation after mating in June—July, delayed implantation occurs in both species. Like the mink, the ferret has only one mating season a year, but, in contrast to what is the case with mink, the length of gestation is very constant.

VOL
28
194

PRESENT INVESTIGATIONS.

From several points of view, experimental investigations on mink are much more difficult than corresponding investigations on, e. g., rabbits, guinea-pigs, mice and rats. One of the reasons is that the mink is difficult to handle, for it is very shy, while at the same time it is also savage. To catch a mink it is therefore necessary to be provided with special equipment and protective gloves of stout leather. These none too favourable characteristics of the mink as an experimental animal can be overcome if experienced keepers are available, who have great skill in handling the animals. On the other hand, the fact that, owing to the great value of the fur, the mink is a costly experimental animal is a greater drawback. As the quality of the fur is at its best during November—January, and as the mating season does not occur until the month of March the killing of an animal during and after the mating season means a considerable financial sacrifice for the owner. For this reason it is necessary to keep the number of animals used within reasonable limits. This is rendered more difficult, however, by the mink's third and most serious drawback as an experimental object in the case of studies of sexual physiology, viz., the short mating season which occurs only once a year. The investigations have to be concentrated within this period, and when, as is often the case, the results obtained in one investigation yield impulses for further studies, these cannot be undertaken until the following year. Therefore such studies of the mink are necessarily very protracted, especially as it is necessary to economise with the animal material.

In an endeavour both to limit the number of animals used and to speed up the investigations, the latter were carried out in stages. To this end, one-year exploratory investigations were carried out on a small scale and on the basis of the results reached more comprehensive investigations were made in the following year, and as a rule were supplemented in the third and fourth years. In spite of this procedure, not until 1946 had the work progressed so far that a collocation of the investigations in their entirety could be made.

Thanks to the courtesy of the Swedish Fur Breeders' Association, the main part of the experimental investigation work was carried out at their experimental farm. Some of the investigations were also made at A. B. Mink, Lidö Säteri, Gräddö, and at A. B. Stenkulla Fur Ranches, Ösmo.

The histological work, which covered a considerable field, was carried out at the Institute of Animal Breeding of the Royal Agricultural College. Thanks to the courtesy of the Director of the Animal Breeding Institute, Wiad, Eldtomta, the statistical work was carried out with the help of the mechanical equipment at the institute.

VOL. 28 947

I. MATERIAL.

The experimental animals were obtained, partly through the Swedish Fur Breeders' Association from its members, and partly from A. B. Mink, Lidö Säteri, Gräddö, and A. B. Stenkulla Fur Ranches, Ösmo. The animals were in a very satisfactory condition, and as a rule of good quality. From all points of view they may be considered representative of the breeding stock of mink in Sweden, and that such animals were made available must be ascribed chiefly to the understanding shown by the mink breeders for these studies.

Of the two breeds, the Quebec mink was more abundantly represented than the Alaska mink. In view of differences of various kinds, the two breeds have been dealt with separately in certain investigations.

A general survey of the range of the experimental material and its distribution over different sets of investigations is given in table 2, in which have

Table 2. *Range of the material and its distribution over different studies.*

Studies of	Number of females		
	Autopsied	Not autopsied	Total
Ovulation	84	—	84
Rate of embryonic development	80	—	80
Female sex organs during anestrus, proestrus	58	—	58
Irradiation	12	70	82
Internal secretion	21	103	124
Total	255	173	428

been included all the animals used in the experiments. Their number was subsequently reduced owing to certain animals having died or having refused to mate, or having been excluded for other reasons.

II. METHODS.

Owing to the varied nature of the work, only the general investigation methods will be described here.

As emerges from table 2, autopsies were made on 255 animals during the course of the work. To kill them, in the majority of cases an electric trap was employed, through which an alternating current of 127 volts could be passed. The interesting observation was then made that pregnant females exhibited greater powers of resistance than did the non-pregnant ones. This tendency was so general that some special cause must be assumed. In a number of cases the animals were put to death by the gases led from a producer gas motor to a box in which the animals were placed. Both methods were satisfactory.

Owing to the great value of the fur and the method of skinning, the animals were always skinned before the sexual organs could be taken out and prepared. The skin was taken off, however, within the course of a few minutes after the animal's death, and therefore this circumstance did not affect the investigations to any extent worth mentioning.

In the histological work all the fixing was carried out in abundant quantities of 10 % formalin solution, immediately after the organs had been taken out and prepared. The sectioning was done after they had been embedded in paraffin. In the great majority of cases, staining was effected with hemalum, the best results being obtained with acid hemalum according to P. MAYER, (ROMEIS 1932). For contrast staining, sometimes eosin and sometimes erythrosin was employed, and both gave similar results on the whole. Possibly the plasma structures appeared somewhat more clearly after eosin staining. In certain cases Azan staining, according to HEIDENHAIN's modified MALLORY's method (ROMEIS 1932), was used in special studies of the general structure of the ovary, tuba and uterus. Especially in the case of the interstitial glandular tissue of the ovary and the granulosa tissues in follicles and corpora lutea, the mordant in this method of staining often had an unfavourable effect on the material. The vaginal smear was always stained with acid hemalum and eosin.

In the case of post-investigations of eggs and embryos, the organs were transferred into a wax vessel filled with the so called KREBS—HENZELEIT's solution. This has the following composition per 1,000 ml of glass distilled water: 6.90 gm NaCl, 0.35 gm KCl, 0.28 gm $CaCl_2$, 0.16 gm KH_2PO_4, 0.29 gm $MgSO_4$ and 2.10 gm $NaCO_3$. While the work was in progress, the wax vessel

was kept at a constant temperature, of 37—38° C, by means of a thermo-element.

When it was necessary to investigate whether there were eggs in the tuba, it was not possible to rinse out the latter, owing to its minute diameter. Instead the tuba was taken out, prepared, and divided into 5—7 segments, which were then extremely cautiously massaged with an iris pincette, whereby the eggs were pressed out of the tuba. This method proved reliable even though it called for meticulous care. Non-implanted eggs or blastocytes in the uterus were obtained by means of cautiously rinsing out with KREBS—HENZELEIT's solution. As a rule they were found in the first drops.

Macro- and micro-photography were employed extensively in the embryological work, the principle being followed that photographing should always take place as rapidly as possible, to avoid changes in the state of the object. When photographs of larger objects were taken, they were immersed in fluids, to avoid the disturbing effect which otherwise readily results on the refraction of the light in the border layer of the organ. On the other hand, photographs of eggs and blastulae were always taken in "hanging drops".

The statistical analysis was carried out in accordance with the methods given by FISHER (1932). In order to avoid repeated descriptions of the degree of significance in the case of different analyses, the probability that other causes than chance play a part are indicated by different numbers of asterisks. Thus when this probability is < 0.95, $0.95 - 0.99$, $0.99 - 0.999$ or > 0.999 this has been indicated by no, one (*), two (**) and three (***) asterisks respectively (cf. BONNIER and TEDIN 1940).

III. ANALYSIS OF BREEDING DATA.

Breeding data from the two breeds Quebec and Alaska mink have been analysed from different points of view to supplement similar investigations made earlier and to obtain a general survey of the reproduction of the mink. Moreover, the statistical analyses were of great value when it was a question of planning the experimental investigations, and also when the results of these investigations were to be interpreted.

A. MATERIAL.

For several reasons, considerable difficulties were associated with obtaining a sufficiently large, reliable and uniform material for the statistical investigations. In the first place at the majority of mink farms, as is the case in the breeding of other animals, no records, or only incomplete records are kept about mating, littering, number of young, etc. In the second, the system

of mating employed greatly affects the breeding data. As a rule the females are tried with the male at the beginning of March, but the date when a start is made varies from farm to farm. Similarly varying systems are employed in the trials. In certain cases the females are tried every day, every other day, every third or sixth, seventh or eighth day, and an unlimited number of matings per female is allowed. In other cases the number of matings per female is limited. On one and the same farm the same mating system is not consistently followed as a rule, but it varies from year to year and from female to female during one and the same year.

At A. B. Mink, Lidö Säteri, where very extensive mink breeding was carried on earlier, a consistent mating system was employed, during the years 1939—41, of testing the females every other day. In 1939 an unlimited number of matings per female was allowed, but during the years 1940—41 only four matings per female were allowed as a rule. The tests were begun at the end of February and continued till the end of March. Careful notes were made of the mating dates, the littering dates, the sizes of the litters and the sexes of the cubs. In 1939—41 a material was collected from this farm comprising 2,403 females of the Quebec breed with 3,543 separate breeding years. As during these years there was no shortage of food, this material can be paid to be fully normal in all respects.

It was not possible to obtain a corresponding material of Alaska mink from that period, as breeding with that breed was then very limited. During the war, however, it made great strides, and therefore it was considered desirable to obtain a comparison material of that breed. Before the 1945 breeding season, special appeals were therefore sent out to 14 selected farms where the Alaska mink was bred, to keep careful records of matings and litters. From 10 of them lists were received giving the breeding data for 548 females. During the year 1944—45 the feeding conditions had improved appreciably in comparison with the years 1942—43, and this material can therefore be described as normal on the whole.

These two materials form the basis for the following elaborations. The total Quebec material has been used in the study of the intervals between the matings and the frequency of matings. In studying the length of gestation this material could no longer be utilized in its entirety, for it cannot be determined with certainty which mating has resulted in fertilization if the female has been mated several times. Therefore, in these cases, only such females have been included as had produced cubs and had been mated once or twice, in the latter case with a maximum interval of two days. As appears from the experimental investigations, these re-mated females are to be looked upon as mated once, as the second mating does not affect the female's estrus condition or ovulation. The number of breeding data among the Quebec material which satisfied these requirements was 697. The Alaska material was collected with the direct object of studying the length of gestation, and therefore the majority of the females, i.e.

VOL.
28
194

494, satisfied the above requirements in respect of mating conditions. These 494 Alaska females, as well as the 697 Quebec females, will be designated below as "once mated" females, to distinguish them from the total Quebec material.

B. MATING SEASON.

Like other species of the Mustelidae family investigated (cf. MARSHALL 1904, PRELL 1927, 1931, 1938, FISHER 1931, SCHMIDT 1932, WATZKA 1940, and WRIGHT 1942 a), the mink has a distinctly defined mating season. When this period is approaching an increasing liveliness can be observed in both males and females. Occasionally typical cooing calls begin to be heard, and females and males exhibit an ever greater interest in each other. This is the outward sign that the sexual phenomena have entered a more active phase.

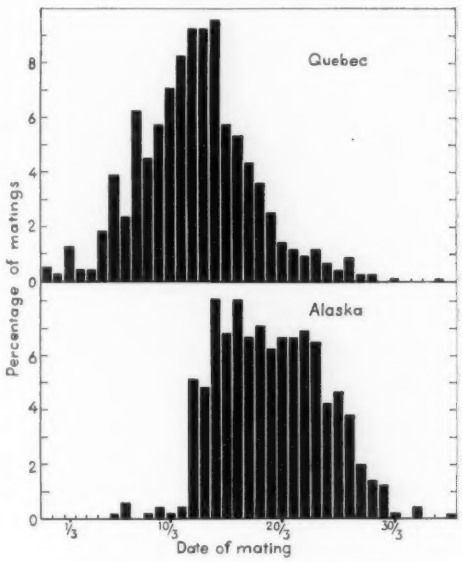

Fig. 1. Seasonal variation of the matings of 697 once-mated Quebec and 494 once-mated Alaska females.

In order to show the time and length of the mating season among the two breeds, the distributions of the dates of mating have been inserted in a diagram (fig. 1). As appears from it, the mating season of the Quebec females occurs earlier than that of the Alaska females, the average mating date being, for the Quebec material, the 12th March and, for the Alaska material, the 19th of March. If one compares the variance in the date of mating between and within breeds a mean square ratio of $\frac{13{,}320.288}{25.462} = 523.1^{***}$ is found. That means that the difference in the position of the mating season cannot be due to chance, but must be due to certain causes. As in the wild state the Alaska breed lives in considerably more northerly latitudes than the Quebec breed, the differences in the dates of the mating seasons are probably due to a genetic adaptation to the climate of the wild populations. From this point of view the two breeds form two ecotypes (cf. TURESSON 1925).

If the diagram is studied more closely, it is found that the Quebec females' mating season is longer than that of the Alaska females. This emerges also from the standard deviation of the mating dates, which, for the Quebec

material, is 5.24, and for the Alaska material, 4.74 days. If the mean squares of the dates of mating within the two breeds are compared a ratio of $\frac{27.432}{22.679} = 1.21^{*(*)}$ is found, which seems to indicate that the difference in standard deviations between the two breeds is due to certain biological causes. There may be many reasons for this difference. In the first place it must be assumed that the temperature or the radiation of the sun, or both, determine the beginning of the mating season, different females coming in estrus at different times, owing to the fact that their sexual functions differ in sensitivity to changes in temperature and light. If the Quebec breed is more heterogeneous in this respect than the Alaska breed, this may be the explanation of the differing lengths of the mating season. This is not necessarily the case, however, for as both the rise in temperature and the radiation of the sun are greatly accelerated during the months of February and March, with the same variation in respect of the sensitiveness of the sexual functions to rises in temperature and to sunshine in the two breeds, the threshhold values for the different females will be passed more rapidly if the mating season occurs late than if it occurs early, and consequently the Alaska females' mating season will be shorter than that of the Quebec females.

VOL
28
194

As the mean temperature during the month of March varied very greatly during the years 1939—41, the once-mated Quebec females have been classified according to the year of mating, for the purpose of investigating the influence of temperature on the time of the mating season. The mean temperature figure for the month of March in the different years was calculated on the basis of information from the Meteorological Institute's station at Väddö, 9 kilometers north of the Lidö Mink Farm, where the temperature was observed at 8 a. m. and at 9 p. m. The mean figures for the dates of mating and the temperature during the three years is shown in table 3. As emerges from this table, in 1939 the females were mated on an average two days earlier than in 1941 and four days earlier than in the unusually cold year 1940. A higher temperature before and during the mating season thus leads to an earlier onset of the estrus. This factor in the case of mink tallies with the result found by JOHANSSON and HANSSON (1940) for the silver fox.

Table 3. *Influence of the temperature during March on the mean date of matings.*

Year	Number of females	Temperature in March	Mean of the mating dates
1939	189	— 0.8	Mch. 10
1940	211	— 5.7	14
1941	297	— 4.8	12

A distribution of the same material according to the ages of the females showed that the mating season began two days earlier for the older females than for the one-year-old ones.

C. MATING HABITS.

The prelude to copulation resembles a chase, which at times becomes somewhat violent, and ends by the male seizing the female with one bite by the

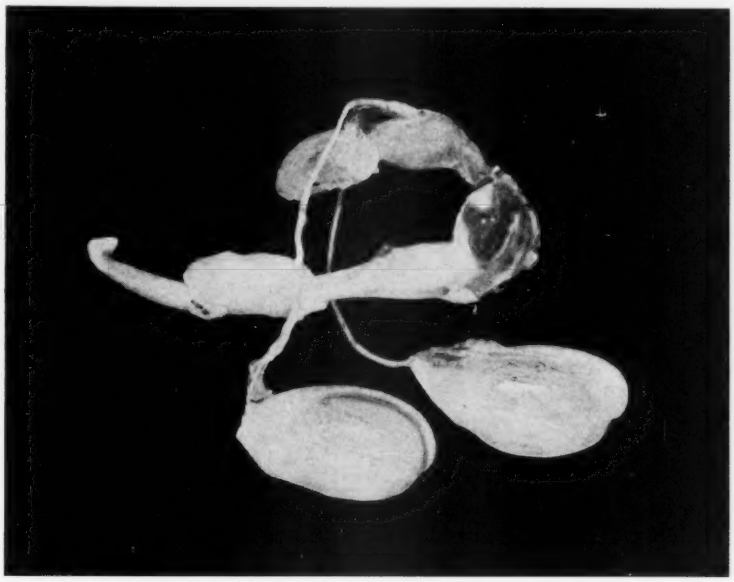

Fig. 2. The sex organs of the mink male during the mating season. (1.2 ×.)

scruff of the neck. He holds her thus, while with his hinder extremities he grips the hind quarters of the female. During actual copulation the male assumes a typical S-shaped position, as does also the female to a certain extent. The act of copulation itself is often very protracted. In one case a period of 14 ½ hours was recorded. It has therefore been considered that the male mink becomes stuck during the act of mating, as happens with dogs, foxes and wolves, owing to intumescent bodies resembling the bulbis glandis (cf. SCHMALTZ 1921). However, copulation can be interrupted at any time, and a macroscopic scrutiny of the penis reveals no such intumescent bodies. In fig. 2 are shown preparations of the sexual organs of a male which was killed during the mating season. The prepuce has been folded back, so that the penis shall be seen better. Its shape is conditioned by os penis, which ventrally has a depression running longitudinally, in which runs the urethra. In front, the

os penis bends round in a dorsal—caudal direction, which gives the penis its harpoon-like appearance. It has not been possible to determine whether this strange configuration is of any importance for mating. The sexual organs of the male mink have not been the subject of systematic investigations, but in their main features they appear to resemble the corresponding organs of ferrets and weasels (cf. ALLANSON 1932 and HILL 1939).

Table 4. *Length of copulation.*

	Length of copulation in minutes						Total
	—30	31—60	61—90	91—120	121—150	151—	
Number of matings	52	70	50	35	13	7	227
Per cent	23	31	22	15	6	3	—

During the experiments, careful records were kept of the length of the matings. This material, which derives from 227 matings, has been arranged in table 4 according to the length of copulation, from which it appears that the length of copulation varies very greatly, or from a few minutes to several hours. The average length for all the matings was 64 mins. In practical mink breeding, it is considered that the matings are longer towards the end of the season than at its beginning. To investigate this question the same material has been grouped in table 5 according to the dates of mating. As appears there is a very clear relation between the dates of mating and the length of copulation. This very interesting phenomenon must be due to a change in the emotional impulses of the animals, as a result of changes either in the estrous state of

Table 5. *Influence of date of mating on length of copulation.*

	Date of mating in March					Total
	—10	11—15	16—20	21—25	26—	
Number of matings	59	60	58	32	18	227
Mean length of copulation in minutes . . .	49	58	62	82	114	64

the female or in the sex urge of the male or in both. As far as can be judged, the prolongation of copulation is not conditioned by a delayed ejaculation of the male, for according to information from A. B. Mink, Lidö, they used to interrupt lengthy copulations intentionally, without its having any effect on the fertilizing effect of the mating. Similarly, during the experiments copulation was deliberately interrupted in two cases, and in both cases examinations of the vaginal secretion revealed sperms.

During one and the same mating season the female usually allows several matings. To illustrate this fact the total Quebec material from 1939, when the

females were allowed to mate an unlimited number of times, has been arranged in fig. 3 according to the number of matings. As is seen, a number of females permitted up to 9 matings during the same season. The average number of matings for all the females was 2.94 per animal. Still more matings would probably have resulted if the females had been tried every day, instead of every other day. The circumstance that during one and the same mating season the female permits several copulations indicates that the mink, in common with e.g. sheep (GRANT 1934), may have several estrous cycles. If such is the case, the interval between the matings would tend to approach a certain value, which would then give the estrous interval. In order to investigate this, in table 6 have been collected, firstly all the intervals between the first and

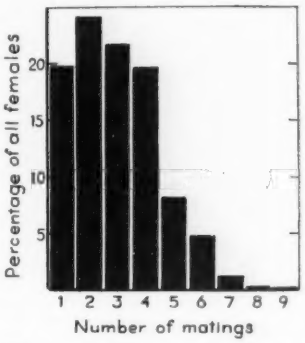

Fig. 3. Frequency distribution of number of matings in 981 Quebec females which were tried with males every other day during the mating season.

Table 6. *Length of the interval between matings.*

	Length of the interval between matings in days									
	1—2	3—4	5—6	7—8	9—10	11—12	13—14	15—16	17—18	19—20
First mating intervals										
Number of intervals	994	205	132	203	310	172	99	23	12	9
Per cent	43.7	9.0	5.8	13.3	13.6	8.0	4.4	1.0	0.5	0.4
All mating intervals										
Number of intervals	2,098	456	388	634	509	285	130	35	17	11
Per cent	46.0	10.0	8.5	13.9	11.2	6.2	2.8	0.8	0.4	0.2

second matings, and secondly all the intervals from the whole of the Quebec material from Lidö. As in this material the females were tried every other day, it has been grouped in two-day groups. As emerges from table 6, the interval centres round two values, viz., 1—2 and 7—10 days. The first cumulation only indicates that the females often allow a second mating before ovulation has taken place after the preceding mating (cf. the experimental investigations). The other cumulation indicates that 7—10 days after a preceding mating the female has a more intensive estrus than immediately before and after. This centering of the mating intervals supports ENDER'S (1940) assumption that the female mink has several waves of follicular maturity, i.e. several estrous cycles, during one and the same mating season. The length of the cycles would then correspond to the interval of the greatest frequency i.e. 8—9 days.

If the two distributions in table 6 are studied, it is found that in the total material when compared with the first mating interval, the second cumulation is somewhat shifted towards the shorter mating intervals. This dissimilarity is due to the fact that in the total material there are several intervals which have been preceded by another mating interval. If this earlier mating interval is 1—2 days, the following mating interval should really not be reckoned as falling between the second and third matings, but between the first and third matings. The distribution which is based only on the interval between the first and the second matings must therefore be considered to give the truest picture of the variation in estrous activity in mink.

Table 7. *Influence of the length of the preceding mating interval on the length of the succeeding mating interval.*

	Length of the preceding mating interval in days							
	1—2	3—4	5—6	7—8	9—10	11—12	13—14	15—16
Number of intervals	1,063	246	199	335	233	119	55	13
Mean length of the succeeding mating intervals in days	6.03	4.60	3.71	3.12	2.75	2.61	2.16	1.85

In table 7 is shown the relation between the lengths of two successive mating intervals. As can be seen, the lengths of the second interval are decreasing as the lengths of the first interval are increasing. The reason for this is that, as the breeding season for every female is of limited duration, after a long mating interval another long interval cannot be expected. Although the relation thus has a trivial explanation and therefore is of but slight interest for the elucidation of the reproduction of the mink; nevertheless it confirms the explanation given of the difference in the nature of the distributions obtained from table 6.

D. SEASON OF PARTURITION.

In fig. 4 is shown the distribution of the dates of littering for the once-mated Quebec and Alaska females. On an average, for the former, parturition occured on the 2nd, and for the latter on 7th May. As the difference in the date of mating was 7 days, this means that, in round numbers, the gestation period of the Alaska females was 2 days shorter than that of the Quebec females. If the standard deviation of the dates of parturition are compared with the standard deviation of the dates of mating, the values 4.9 and 5.2 are found for the Quebec material and 4.4 and 4.7 for the Alaska material. Thus for both breeds the date of copulation shows a greater variation than the date of parturition.

E. LENGTH OF GESTATION.

As is the case with the majority of biological phenomena, the length of gestation, too, shows a clear variation in all animals, due to chance or definite causes. The absolute magnitude of this variation is closely connected with the actual length of gestation, in that animals with long gestation periods exhibit a greater variation than animals with shorter gestation periods. As appeared from the introductory discussion of the literature, the length of the gestation of the mink varies very greatly. In table 8 and fig. 5 the gestations from the once-mated Quebec and Alaska females have been inserted. Its average length in the former is 51.33 days, with a standard deviation of 5.42 days. The distribution exhibits a significant skewness, $S = -0.585^{**}$, and excess $E = 0.057^{*}$. The average length of the gestation of the Alaska females is 49.01 days, with a standard deviation of 4.18 days. In this case the skewness is less pronounced, $S = -0.167^{**}$, but on the other hand the excess is greater, $E = 0.118^{**}$. The coefficient of variation is 0.1057 for the Quebec females and

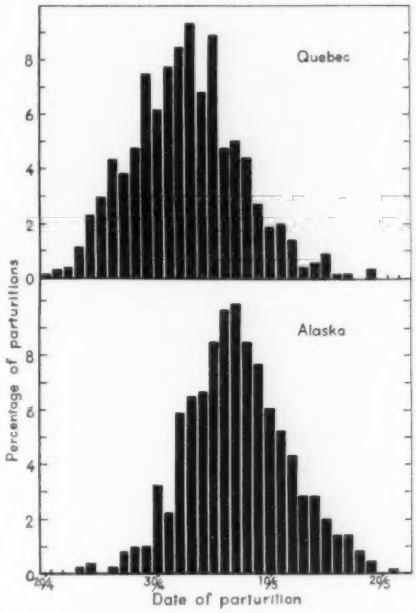

Fig. 4. Seasonal variation of parturition in 697 Quebec and 494 Alaska females.

Table 8. *Length and variation of the gestation period.*

	Length of the gestation period in days									Total and mean
	39–42	43–46	47–50	51–54	55–58	59–62	63–66	67–70	71–74	
Quebec:										
Number of gestations .	16	109	223	183	94	45	20	6	1	697
Per cent, (days) . . .	2.3	15.6	32.0	26.3	13.4	6.4	2.9	0.9	0.1	(51.3)
Alaska:										
Number of gestations .	27	117	172	129	38	8	3	—	—	494
Per cent, (days) . . .	5.5	23.6	34.8	26.1	7.7	1.6	0.6	—	—	(49.0)
Total:										
Number of gestations .	43	226	395	312	132	53	23	6	1	1191
Per cent, (days) . . .	3.6	19.0	33.2	26.2	11.1	4.5	1.9	0.5	0.1	(50.3)

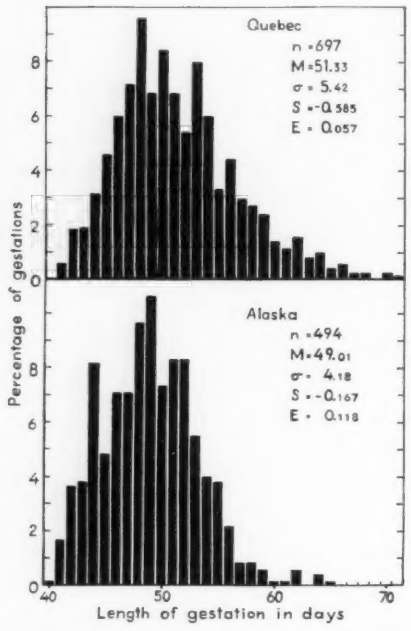

Fig. 5. Frequency distribution of the length of gestation for 697 once-mated Quebec females and 494 once-mated Alaska females.

0.0853 for the Alaska females. The results as regards the length and variation of gestation thus show complete conformity with those obtained earlier by KELLER (1937), FUNKE (1939), ENDERS (1940), JOHANSSON (1940), APELGREN (1941), BOWNESS (1942) and PEARSON and ENDERS (1944).

In order to be able to judge the relative magnitude of the variations in mink as regards the length of gestation, material from other kinds of animals has been collected in table 9, the animals being arranged according to the mean length of gestation. If a comparison is made between the length and the variation of the gestation period, it is found that they change in the same direction. The coefficient of variation therefore has a fairly constant value for the majority of the animals. However, the mare has a somewhat higher, and the sheep, silver fox and ferret a somewhat lower coefficient. The average length of gestation in mink varies from 49.1 to 51.3 days, i.e. a period corresponding to that of the silver fox. The standard deviation is, however, 5 or 6 times as great. If the coefficients of variation are compared, it is found that in mink it is about three times as great as that of the mare and four to six times as great as those of the other kinds of animals. Thus this comparison shows that the gestation period of the mink exhibits enormous variation in comparison with that of other domestic animals, and therefore there is reason to expect that special conditions assert themselves in the case of the mink.

It is customary to speak of a normal and an abnormal variation in the length of gestation. By the former is then meant, firstly random variation, and secondly non-random variation which is due to normal causes, such as the number of foetuses, their sex, and the season. On the other hand, by abnormal variation is meant the premature or delayed birth due to external influences, undernourishment, infections of various kinds, such as contagious abortions or pathological defects in the foetuses. In many cases it is difficult or impossible to draw a sharp border-line between normal and abnormal variation. Only the normal variation according to the above definition will be dealt with below.

Investigations by JOHANSSON (1928), AXELSSON (1929), HINTERTHÜR

VOL
28
194

Table 9. *Length and variation of gestation for different animals.*

Animal and breed	Number of gestations	Gestation			Authors
		Mean length in days	Standard deviation	Coefficient of variation	
Horses: Light and heavy breeds, ♂-foal	5,709	334.1	9.45	0.0283	Uppenborn (1933)
Horses: Light and heavy breeds, ♀-foal	5,552	332.5	9.55	0.0287	„ (1933)
Cattle: Swedish Red and White cattle	10,219	283.7	5.76	0.0203	Johansson (1928)
Cattle: Swedish Friesian cattle	2,682	278.8	5.04	0.0181	Axelsson (1929)
Goats: Anglo-Nubian	6,342	150.9	3.33	0.0221	Asdell (1929)
Sheep: Merino	360	149.0	2.16	0.0145	Sabatini (1908)
Shropshire	350	145.6	2.22	0.0152	„ (1908)
Swedish breeds	486	144.9	2.73	0.0188	Rydå (1945)
Pig: Large White Yorkshire	1,423	114.3	2.40	0.0210	Johansson (1938)
Swedish Landrace	506	115.1	1.50	0.0130	Åbjörnson (1936)
Fox: Silver fox	587	52.0	0.88	0.0169	Johansson (1938)
Blue fox	969	52.2	1.06	0.0203	„ (1945)
Ferret	25	42.0	0.34	0.0081	Hammond and Marshall (1930)
Rabbit	888	31.1	0.83	0.0267	Nachtsheim (1935)
Mink: Quebec	264	50.8	(41—68)	—	Johansson (1940)
American breeds	747	51.0	(39—76)	—	Bowness (1942)
„ „	233	51.0	5.3	0.1039	Pearson and Enders (1944)
Quebec	697	51.3	5.42	0.1057	Own investigations
Alaska	494	49.0	4.18	0.0853	„ „

(1933) and Mauch (1937) have proved that in horses, cattle, and possibly pigs, there is a tendency towards protraction, and in goats a tendency towards curtailment, of gestation with increasing age of the mother. It has not been possible to prove any such relation in the case of mink from the material which has been studied.

Investigations by Husby (1933) and Hammond (1934, 1936, 1937) proved that in pigs and rabbits there is a clear tendency towards a shortening of the gestation period with an increasing number of foetuses. Similar investigations on horses, cattle, sheep and goats by Sabatini (1908), Johansson (1928), Axelsson (1929), Asdell (1929), Hinterthür (1933), Uppenborn (1933), Mauch (1937) and Orlovskiĭ (1940) showed, firstly, that gestation is somewhat longer for male than for female foetuses, and secondly that gestation is shorter in the case of twin births than in that of a single birth.

Table 10. *Influence of size of litter on length of gestation.*

	Size of litter				
	1—2	3—4	5—6	7—8	9—10
Quebec: Number of gestations	119	259	244	72	3
Mean length of gestation in days	52.5	51.6	50.4	51.7	49.3
Alaska: Number of gestations	54	120	198	106	16
Mean length of gestation in days	49.5	49.9	48.4	48.8	50.5

The relation between the number of young produced and the length of gestation in mink was studied on the basis of data for the once-mated Quebec and Alaska females. From table 10, where the results of this investigation have been collected, it emerges that there is a certain tendency, even though an irregular one, towards a shortening of gestation with an increasing number of young. The correlation between the two variables is $r = -0.119^{**}$ for the Quebec and $r = -0.084^{*}$ for the Alaska females.

The relation between the number of young born and the length of gestation has been assumed by several workers to be due to the fact that, with more foetuses in the uterus, the intrauterine pressure is increased, whereby the onset of partus is hastened. It does not appear probable, however, that this explanation contains the whole truth, for probably endocrine factors play the main part. In mink the chief cause of the relation will probably be that, as the interval between ovulation and implantation shows a great variation (cf. section VI), and as during that period the embryos have no intimate contact with the uterus mucosa, in the case of long gestations an increased intrauterine mortality is to be expected, which would lead to a negative correlation.

Investigations by JOHANSSON (1928), AXELSSON (1929), HINTERTHÜR (1933), UPPENBORN (1933), MAUCH (1937), ORLOVSKIĬ (1940) and SWEČIN (1941) have proved that for mares, cows and goats there is a relation between the date of mating and the length of gestation. This relation is particularly marked in mares but is more uncertain in cows and goats. These animals differ greatly from the mink, however, in respect of the sexual cycle, and the influence of the mating date which asserts itself in these animals is probably also conditioned by entirely different factors from those in the case of mink. As the relation between the length of gestation and the date of mating in mink is of very great interest, this relation has been analysed on the basis of the once-mated Quebec and Alaska females. In table 11 the material has been classified into 4-day groups according to the date of mating, and for each group the average length of the gestation period has been computed. As appears from the series of figures, for the Quebec and Alaska females there is a very clear and consistent relation between the dates of mating and the lengths of gestation.

Table 11. *Influence of date of mating on length of gestation.*

Date of mating	Quebec		Alaska		Total	
	Number of females	Mean length of gestation	Number of females	Mean length of gestation	Number of females	Mean length of gestation
Mch. — 4	38	60.3	—	—	38	60.3
5— 8	118	54.7	5	53.9	123	54.7
9—12	210	52.0	30	51.3	240	51.9
13—16	207	49.4	138	51.5	345	50.2
17—20	82	48.1	132	49.2	214	48.8
21—24	27	46.4	120	47.0	147	46.9
25—28	13	46.8	59	46.0	72	46.1
29—	2	46.0	10	45.1	12	45.3

VOL. 28 1947

The two materials have, therefore, been pooled, and on the basis of the new average values a second degree curve has been fitted. This yields the function $y = 62.0 - 1.0846x + 0.01804x^2$, where y is the length of gestation and x the mating date in March. Fig. 6 shows this curve with the averages inserted. As appears, the length of gestation decreases greatly when the date of mating is moved forward. At the beginning of the mating season the length of gestation decreases more rapidly than towards the end. From the beginning to the end of March gestation is shortened by nearly 15 days (cf. FUNKE 1939, BOWNESS 1942, PEARSON and ENDERS 1944).

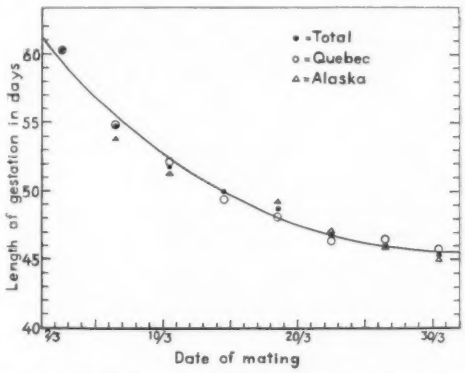

Fig. 6. Relation between date of mating and length of gestation in 697 once-mated Quebec females and 494 once-mated Alaska females and in the total 1,191 females.

The significance of this covariation may also be shown by an analysis of variance of the Quebec material. (The Alaska material, which was collected from 10 different farms, was considered too heterogenous for such an analysis.) In order to eliminate the differential influence of the different years, the comparisons (table 12) are made within years. The order of magnitude of the mean square ratio proves the high significance of the correlation between dates of mating and lengths of gestation. The analysis shows also that the part of the variance within years of the lengths of gestation, which is due to differences in dates of mating may be estimated to be $\frac{29.12 - 17.51}{29.12}$ or 39.87 per cent. The error mean square (17.51) gives a standard deviation of 4.18

Table 12. *Analysis of variance of length of gestation.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Ratio of mean squares
Between years	2	30.0	15.00	
Within years	694	20,211.1	29.12	$\frac{126.43}{17.51} = 7.22^{***}$
Between date of mating	74	9.355.8	126.43	
Within date of mating (error) .	620	10,855.3	17.51	
Total	696	20,241.1	29.08	

and a coefficient of variation of 0.0816. If the latter is compared with the corresponding coefficients in table 9, it is found that the variation in length of gestation is still several times greater than for other animals. Thus the date of mating is certainly the cause of a considerable part of the variation, but there must still be important causes of variations which cannot be disclosed by a statistical analysis.

F. CONCLUSIONS.

Analysis of breeding data has shown, in full agreement with earlier investigations by FUNKE (1939), ENDERS (1939, 1940), JOHANSSON (1940), APELGREN (1941), BOWNESS (1942), BAHLCKE (1944), PEARSON and ENDERS (1944) and STEVENSON (1945), that the reproduction of mink has several strange features. Thus the time of the mating season is affected by the temperature before and during that period. Further there is a general trend in the length of the copulations in relation to dates of mating. During one and the same mating season, the females also allow several matings, and the intervals between these matings tend to centre round the values 1—2 and 7—10 days, thus indicating a cyclic estrous activity. Further, there is a very great variation in the length of gestation, the coefficient of variation being 3 to 6 times as great as that for other kinds of farm animals. The date of mating has a very pronounced influence on the length of gestation. In fact, after mating in the beginning of March, the gestation period is nearly 15 days longer than after mating at the end of the same month. In spite of the great influence of the date of mating on the length of gestation, yet there must be special causes of variation in the length of gestation in the mink, which cannot be revealed by statistical analysis of breeding data.

VOL
28
194

IV. GENERAL ANATOMICAL SURVEY.

The anatomy and histology of the female sexual organs in mink have not been previously subjected to study. For this reason the material secured in connection with the experimental investigations of ovulation and embryonal development, supplemented with material collected during anestrus and proestrus, was made the basis of an anatomical-histological study. In this section, however, only a general anatomical survey is presented. The changes in the sexual organs which are correlated with the sexual cycle are discussed in connection with ovulation and implantation. The nomenclature in this study has been brought into line with that employed by ALLEN, DANFORTH and DOISY (1939) and MAXIMOW and BLOOM (1943).

OL.
28
947

A. ARRANGEMENT OF THE FEMALE SEX ORGANS.

In the abdominal cavity each uterine horn with its tuba lies in a long fold of the peritoneum, the ligamentum lata, which is completed cranially by the plica mesonephridica. The ligementum lata runs dorsally from the abdominal wall, somewhat laterally of the medial plane of the body, and is caudally, mainly dorso-ventrally, directed, but cranially it takes a more dorso-latero-ventral direction. The plica mesonephridica, which originally formed the ligament for the mesonephros, proceeds from the dorsal diaphragm region and runs, laterally to the kidney, to the hilus of the ovary, where some of the muscle fibres enter the medullary zone of the ovary, and others spread out into the bursa ovarii. From the hilus of the ovary this ligament continues to the uterine horn under the designation "ligamentum ovarii proprium". The latter is so short that the ovary is fixed in the immediate proximity of the utero-tubal junction (fig. 7 and 9). As a result the tuba in mink, as also in ferrets (MURR 1935), has an extremely characteristic course (fig. 9). From the utero-tubal junction the tuba runs round the ventral surface of the ovary in the cranio-medio-caudal direction, and during its course forms 10—11 regular coils. The infundibulum thus comes to lie in the immediate proximity of—but medially to—the utero-tubal junction. In mink, too, the mesotubarium is divided, owing to the fact that the tuba does not lie in the marginal zone of the ligament but dorsally to it, into a mesotubarium inferius and a mesotubarium superius. In contrast to the state of things in mice (AGDUHR 1927), mesotubarium superius also enters into the formation of the bursa ovarii. This ligament extends as a thin transparent membrane over the ventral side of the ovary (fig. 9). Dorsally to the tuba, the mesotubarium inferius, the mesovarium,

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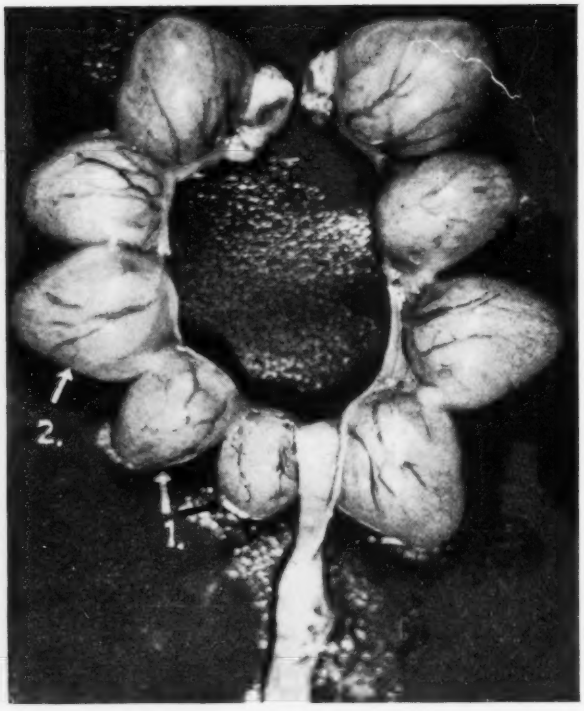

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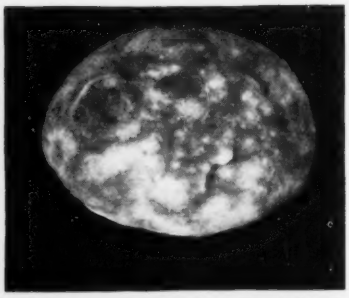

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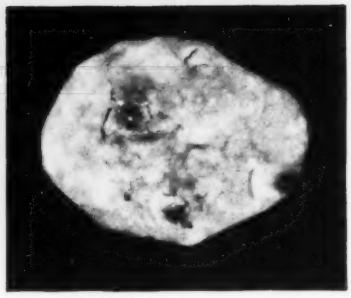

11

VOL.
28
194

and the plica mesonephridica, form an irregularly cone-shaped continuation of the bursa ovarii. This formation is surrounded by large accumulations of subserous fat. These so-called corpora adiposa were considered by AGDUHR (1927) to be of importance as a protection for the ovaries. The correctness of this hypothesis cannot be confirmed, but it is significant that even very emaciated females still have well developed corpora adiposa, which indicates that these are not to be looked upon only as fat deposits. The ovarian pocket is not completely closed as in mice (ROBINSON 1887, AGDUHR 1927), but, as is the case with ferrets (ROBINSON 1918), with a fine style a connection can be shown, the ostium abdominale, between the bursa ovarii and the abdominal cavity. In some females it was not possible to prove such a connection, but in several of these cases secondary adhesions were met with at the same time between different parts of the ligamentum lata and between the latter and other ligaments in the abdominal cavity. This indicates that such adhesions may also have occurred in the ostium abdominale.

The part of the ligamentum lata in which the corpus uteri and the cornua uteri lie, or the mesometrium, consists of two long membranes, which, in the corpus uteri and the cervix, start from the outer dorsal-lateral edge.

B. OVARY.

As a rule the ovary of the mink is bean-shaped and has a relatively smooth surface, even during the follicular and corpora lutea phases (fig. 10 and 11). The surface is covered with a simple cuboidal germinal epithelium. At the hilus of the ovary the germinal epithelium passes over at a marked border-line into the mesothelium of the peritoneum, the cells of which are squamous in character.

Between the germinal epithelium and the underlying connective tissue, the tunica albuginea, there is no basement membrane. The tunica albuginea, which, with the exception of the hilus, forms a capsule of connective tissue round the ovary, consists of spindle-shaped cells and fibrils, which run mainly parallel with the surface of the ovary. At intervals strands from the albuginea bend inwards to become continuous with similar strands in the cortex.

The medulla of the mink ovary is limited to the region of the hilus of the ovary, and its relative size is less than in the case of ferrets (ROBINSON 1918),

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Figs. 7—11. — 7. The female sex organs during the free vesicle stage. Note that the uterine horns were a little contracted at the moment of photographing. (1.0 ×.) — 8. The female sex organs during pregnancy. The female was autopsied 30 days after mating. *1.* Implantation site containing a foetus which undergoes resorption. *2.* Implantation site containing a pair of identical twins. (1.0 ×.) — 9. Bursa ovarii with tuba uterina and the proximity of the uterine horn (8.2 ×.) — 10. The ovary immediately before ovulation. Note the follicles ready to ovulate. (8.2 ×.) — 11. The ovary immediately after ovulation. Note the ovulation ruptures. (8.2 ×.)

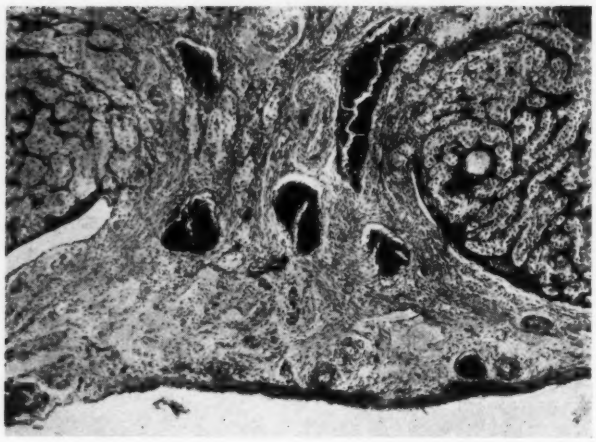


Fig. 12. Section through the hilus of the ovary. Note the distinct border-line between the medulla and cortex. (Azan stained, greenfilter, 60 ×.)

VOL. 28 194

the ovaries of which otherwise correspond closely to those of the mink. As is partly shown by fig. 12, the medulla consists of loose connective tissue and large contortuous blood vessels, lymph spaces and strands of smooth muscle fibres. During the active sexual period, pro-estrus to parturition, there is reason to characterize the medulla as a zona vasculosa, on account of the great development of the vascular system. Contrary to what is the case in the majority of the other animals studied, it is possible in the case of mink to speak of a marked borderline between the medulla and cortex. It is true that the connective tissue, and the vessels and nerves in the cortex, form a continuation of corresponding structures in the medulla, but in the cortex still another tissue is met with, which dominates the microscopic picture, namely the interstitial glandular tissue. This tissue forms a sharp borderline between the cortex and medulla. If a section through the cortex is studied, it is found that it is divided, by connective tissue lamellae running in different directions, into a large number of irregularly shaped columns and nests, which give the ovary a strikingly labyrinthine appearance (fig. 13). As ROBINSON (1918) found in ferrets, primitive follicles generally lie in and close to the connective tissue lamellae, which bend into the cortex from the tunica albuginea. This is the case also with the vesicular follicles and corpora lutea, but in the case of the latter this topographical correlation is less obvious, owing to their greater diameter.

The abundance of interstitial glandular tissue in the mink ovary indicates that it has a special task. HOLMSTRÖM (1920) states that this tissue is met with chiefly in "lower forms of mammals with non-periodical ovulation". MAXIMOW and BLOOM (1943) say about this tissue: "It has not been possible to separate these tissues from other constituents of the ovary, and so no con-

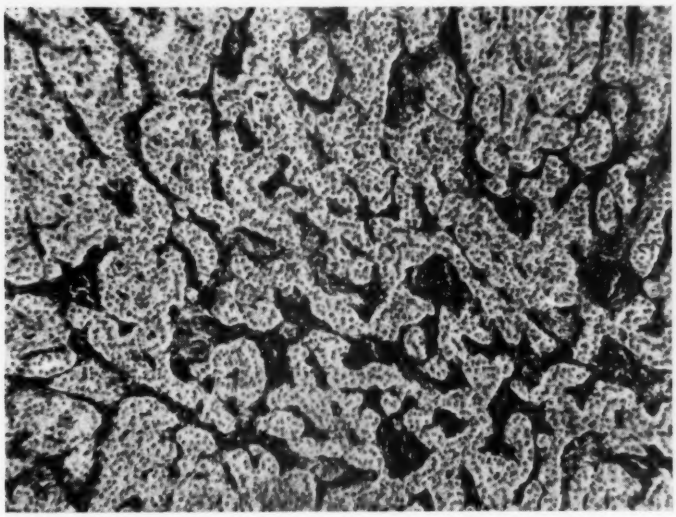


Fig. 13. Section through the cortex of the ovary. Note the arrangement of the interstitial glandular tissue. (Hemalun-eosin stained, redfilter, 100 ×.)

vincing evidence has been obtained by methods of extraction or of implantation". The circumstance that in mink anestrus lasts from May to January, during which period no follicular growth beyond the vesicular stage takes place, indicates that during that period the interstitial glandular tissue may serve as a regulator in governing the sexual differentiation. With the object of throwing light on the origin of the interstitial glandular tissue, concerning which there is a great confusion of ideas, special studies of its histogenesis in mink have been begun, for which reason this interesting and important question will not be further dealt with in this work.

C. TUBA UTERINA.

Owing to its fixed position in relation to the ovary and cornua uteri and to the practically closed bursa ovarii, the tuba in mink never attains the same degree of differentiation as is the case in the majority of the animals studied. It is true that the infundibulum with its fimbria, the dilated ampulla and a narrower isthmus, which passes into the tubo-uterine junction, can be distinguished, but the fimbriae in particular are very slightly developed. As WESTMAN (1926) pointed out, there is probably a negative correlation between the development of the bursa ovarii and the development of the fimbriae. Animals with a well developed bursa ovarii, such as mink, mice, rats and dogs, have slightly developed fimbriae, while animals with slightly developed bursa ovarii, such as apes, cows, mares, sows, etc., have well developed fimbriae.

In mink the tuba varies in length from 10 to 15 mm and its external diameter is about 1.0 mm in the ampulla and 0.6 mm in the isthmus. In the cornua uteri, the tuba opens at the end of a papilla. At the junction there is also a definite smooth-muscle sphincter. In several respects the tubo-uterine junction in mink conforms closely to the corresponding formation in cats and hedgehogs (ANDERSEN 1928).

Externally the tuba is surrounded by the serosa and subserosa of ligamentum lata. In the infundibulum and ampulla the subserosa attains considerable thickness. The tunica muscularis in mink also consists of two layers, namely an outer longitudinal one and an inner circular or spiral one. The longitudinal layer occurs in more or less discrete bundles round the tuba which connect up with strands of muscle fibres from the mesotubarium. In different parts of the tuba the two layers of tunica muscularis attain very different degrees of development. In the infundibulum and ampulla the longitudinal layer is very well developed, while the circular layer is extremely little developed. On the other hand, in the isthmus, and especially towards the tubo-uterine junction, the circular layer is very thick, while the longitudinal layer is strikingly little developed. It appears probable that this dissimilar development of the two layers of tunica muscularis in different parts of the tuba is connected with their antagonistic effect, and that this is one reason why the egg passes considerably more rapidly through the anterior part of the tuba than through the posterior part.

The mucosa exhibits a striking picture in cross section. It is thrown up into several longitudinal folds, which, in the infundibulum and ampulla, have secondary and tertiary folds, giving the cross-section a complex labyrinthine appearance. Secondary channels formed by interdigitating folds intercommunicate and also open into the central lumen. In the isthmus the mucosa is less complex, and in the intramural portion there are only a few slight folds.

D. UTERUS.

The long, tapering uterine horns of the female mink fuse immediately in front of the cervix and form a rudimentary corpus (fig. 7). The cervix has a well developed circular muscular sphincter and the cervical canal opens into the vagina on a somewhat dorsally projecting papilla. The arrangement of the different tissue-layers in the uterus of the female mink conforms in most cases with conditions in other mammals. Thus the serosa and subserosa are formed by the ligamentum lata, from which vessels, nerves and strands of muscle fibres run downwards and ramify into the cornua and corpus uteri. Tunica muscularis consists of a longitudinal and a circular layer. During anestrus the mucosa forms four long, low folds and contains numerous uterine

VOL
28
194

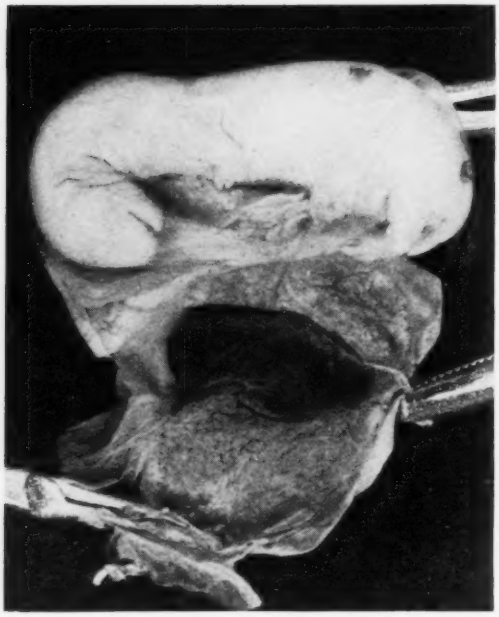
glands. At the transition to and inside the cervix itself, the mucosa and its folds are considerably lower, and the uterine glands occur only sparsely.

E. PLACENTA.

If the female is mated, and the eggs are fertilized and implanted, the typical changes connected with placentation which are found in all animals with a placenta vera, are also found in mink. The placenta of the mink almost conforms to the corresponding formation in the species of Mustelidae studied by STRAHL (1889 and 1906), STRAHL and BALLMAN (1915) and RAU (1925). The placentas of ferrets especially, which are described in detail by STRAHL and BALLMAN (1915), correspond very closely with the placentas of mink.

In mink the placenta at first develops like a placenta zonaria, but the trophoblast layer of the blastula forms no villi in the mesometrial region and only inappreciable villi in the central part of the antimesometrial region. The placenta therefore becomes discoidal in shape, and, as STRAHL (1906) suggested in the case of ferrets, in view of its original shape, there appears to be reason to characterize it as a placenta zonodiscoidalis. The remarkable extravasate accumulations, which, according to STRAHL (1889), BISCHOFF first proved in Putorius furo, are also met with in mink. They show themselves macroscopically when the implantation site is opened from the mesometrial side, first as a darker area in the central part of the antimesometrial region of the placenta. At this point of time the whole implantation site is fully the size of a pea. The area in the antimesometrial region gradually becomes increasingly dark in colour, and by degrees an aggregation of swellings is formed in its centre. At a certain point of time this aggregation consists of a clearly stalked and lighter formation, hardly the size of a hemp seed, which is surrounded by smaller non-stalked and darker swellings in the allantochorion. The whole of this aggregation gradually becomes more homogeneous, at the same time as it increases in size and resembles a spleen in appearance. In fig. 14 is shown an opened implantation site at this point of time. The foetus in situ lies with its back turned to the extravasate accumulation or haematoma, but in order to obtain a better picture it has been lifted up out of the placental cavity. As can be observed on the picture, the allantois stalk with the umbilical vessels enters the placenta in immediate proximity to the haematoma.

As regards the formation of these haematomas, according to STRAHL (1889), BISCHOFF assumed that they originated as a result of ruptures in the allantois vessels of the foetus in the antimesometrial region, and that these ruptures were due to the weak development of the villi of the ectoderm. STRAHL (1889) was able to prove, however, that the red blood corpuscles found in the extravasation were smaller and lacked the fragments of nuclei characteristic of



14

15

Figs. 14—15. — 14. An opened implantation site. Note the large spleen-like heamatom in the centre of the placenta. (1.0 ×.) — 15. Section through the placenta. In the upper part of the section a foetal vessel. In the lower part of the section a maternal vessel. Note the differences in erythrocytes and in the height of the endothelial cells. (Hemalun-eosin stained, redfilter, 600 ×.)

embryonal blood corpuscles. On the other hand, they were identical with the mother's red blood corpuscles. In the mink placenta it is easy to distinguish between the blood capillaries of the mother and those of the foetus, for in the former the endothelium is greatly thickened (fig. 15). If the erythrocytes in the mother's capillaries are studied, it is found that, in the first place, they are considerably smaller than those of the embryo, and in the second, that their shape has been greatly influenced by the histological treatment, which is not the case with the erythrocytes of the foetus. The maternal erythrocytes are met with in the extravasate, and this confirms STRAHL's observation that the haematomas arise owing to ruptures in the maternal capillaries.

RAU (1925) showed that these haematomas occur in different forms in dogs, cats, bears and ferrets. Their physiological purpose is still obscure, but the circumstance that in dogs and cats the extravasates contain abundant haemoglobin, and in ferrets and mink haematoidin crystals, indicates that the haematomas may promote the supply of haemoglobin to the foetus. The trophoblast cells which coat the embryonal villi protruding into the extravasate also exhibit a conspicuous phagocytosis both in ferrets, (STRAHL 1889, 1906, STRAHL and

BALLMAN 1915) and in mink. In the latter these cells contain not only haematoidin crystals, but also maternal erythrocytes. The haematoma reaches its maximal development some time before parturition, to be almost entirely resorbed later. This indicates that the foetus becomes independent of the mother in respect of supplies of haemoglobin before parturition takes place.

With regard to the structure of the placenta, reference should be made to STRAHL and BALLMAN (1915), whose description of the placenta of ferrets also applies to that of the mink.

V. OVULATION.

A. FOLLICULAR DEVELOPMENT.

The growth of the follicles bears such an intimate relation to the ovulation phenomena that it has been considered necessary to study the follicular development in mink in connection with ovulation. On the other hand, it is outside the scope of this work to study the question of the germ plasm, and therefore reference should be made to EVERETT (1945), who gives an excellent review of the present position of the germ-cell problem as regards vertebrates.

In earlier investigations, which were reviewed in detail by ROBINSON (1918), it was mainly the structure of the follicles that was studied, but very seldom the progressive changes in follicular development. In the case of ferrets, however, ROBINSON (1918) has given an extremely detailed description of follicular growth during the vesicular stage, and BRAMBELL (1928), PARKES (1931), PINCUS (1936), DEMPSEY (1937), PINCUS and ENZMANN (1937), and DAWSON and FRIEDGOOD (1940), have given detailed descriptions of the relation between ovum growth and follicular growth in mice, guinea-pigs, rabbits and cats. With the exception of ROBINSON and PARKES, they have also correlated the various morphological types of follicles with the corresponding ovum stages.

The writer has made a corresponding analysis for mink. The method was as follows: after a careful study of follicular growth it was considered possible to divide the development from the primitive follicles—which consist of an ovum surrounded by disconnected flattened cells, to the full-grown follicles ready to ovulate—into nine different stages according to the following scheme:

Stage 1. In the germinal epithelium, there can now and then be observed cells which are larger, less stainable, and consequently lighter than the other cells. Probably these cells are the progenitors of the primary oocytes (cf. LATTA and PEDERSEN 1944, and EVERETT 1945). When these cells have migrated from the germinal epithelium they are found surrounded by a disconnected layer of flattened cells, which constitute the primitive capsule, and which are

the progenitors of the follicular epithelium. These primitive follicles generally lie in aggregations in the tunica albuginea or in the strands of connective tissue, which turn inwards into the cortex.

Stage 2. This stage is distinguished from the preceding one by the still flattened epithelial cells forming a connected membrane round the egg (fig. 16).

Stage 3. Apart from a further growth of the egg, this stage is characterized by continued proliferation in the epithelial layer, which has led to the formation of a compact single layer of cubic epithelial cells round the egg (fig. 16). At the same time, outside this layer a differentiation can be established of the surrounding spindle-shaped cells, which is the prelude to the formation of a theca layer. Even at this stage the occurrence of a definite basement membrane can be established between the inner layer of epithelium and the connective tissue capsule. At the same time an oolemma or zona pellucida begins to develop round the egg, which, as pointed out by PINCUS and ENZMANN (1937), appears to take place with the help of the surrounding epithelial cells, the latter being attached to the oolemma by means of numerous protoplasmic structures.

Stage 4. By continued cell proliferation in the epithelial layer a two-layered stratum has been formed (fig. 17). In the theca layer the differentiation has proceeded, so that this layer now consists of a theca externa and a zona vasculosa or theca interna. The zona pellucida exhibits a further increase in thickness and is connected by means of protoplasmic strands, not only with the epithelial cells lying nearest, but also with the outer layer of cells. A very appreciable change in the shape of the follicle can be observed. In the earlier stages both the egg and the follicle were spherical in shape, but the majority of the follicles and eggs are now of a typical ovoid form.

Stage 5. As a result of continued cell proliferation, a multilayered stratum of epithelial cells has formed round the egg. The oolemma has attained considerable development, and there is an indication of a differentiation of a special cell-layer round the egg. Instead of lying in the tunica albuginea as it usually did before, the follicle is now generally found in the cortex.

Stages 2—5 correspond to the secondary follicle stage as described in earlier literature (cf. SAND 1918).

Stage 6. Characteristic of this stage is the incipient formation of antra. This

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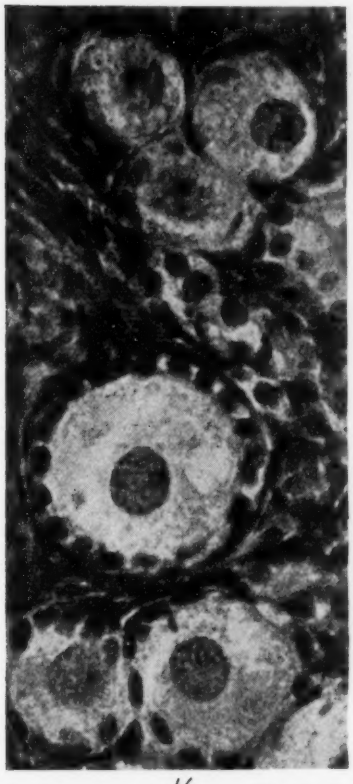
Figs. 16—20. — 16. Section through a nest of follicles in tunica albuginea showing follicles at different stages of development. (Hemalun-eosin stained, redfilter, 600 ×.) — 17. Section through a follicle in which the granulosa consists of two layers of cells. (Hemalun-eosin stained, redfilter, 300 ×.) — 18. Section through a follicle in the stage of incipient antrum formation. (Hemalun-eosin stained, redfilter, 150 ×.) — 19. Section through a follicle with an almost homogeneous antrum folliculi. Note the protoplasmic strands running through the liquor folliculi. (Azan stained, greenfilter, 180 ×.) — 20. Section through a follicle which is almost ready to ovulate. (Azan stained, greenfilter, 50 ×.)

VOL.
28
194



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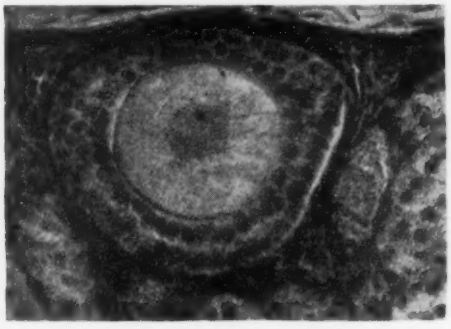

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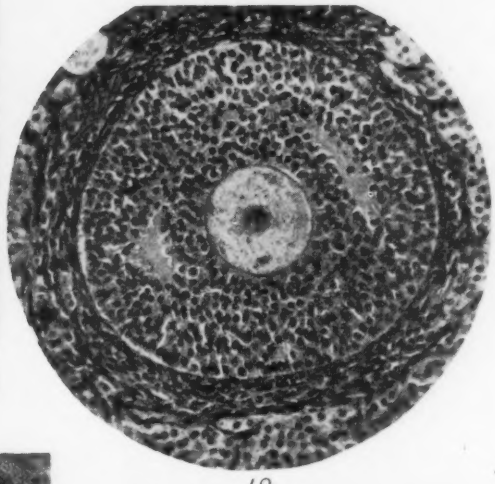

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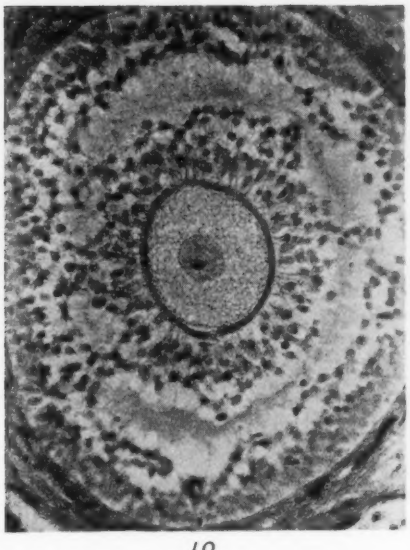

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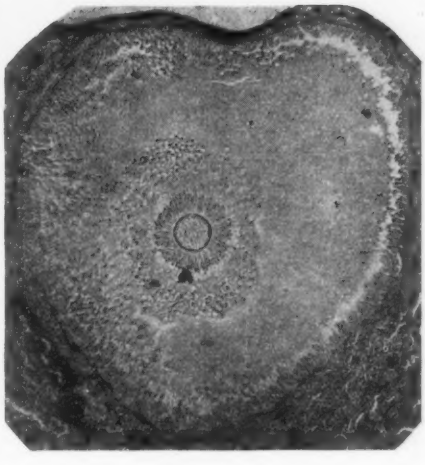

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first shows itself, as ROBINSON (1918), BRAMBELL (1928), PINCUS (1936) and PINCUS and ENZMANN (1937) also found, in the poles of the follicle (fig. 18). In the latter, small cystiform cavities appear between the epithelial cells and gradually merge into larger units. These cavities are filled with follicular fluid, through which run protoplasmic strands from the adjacent cell territories. ROBINSON (1918) has proposed the designation "primary liquor folliculi" for this fluid. Simultaneously with this differentiation in the granulosa layer, the theca layer has definitely developed into two layers. The outer layer, the theca externa, consists of a dense connective tissue capsule of spindle-shaped cells and fibrils. The inner layer consists of loose connective tissue with interspersed polygonal cells, which recall the cells in the interstitial glandular tissue and contorted blood vessels and lymph sinuses.

Stage 7. Owing to a continued incretion of follicular fluid, the vacuoles in the granulosa tissue described in the preceding stage are united into a homogeneous antrum folliculi (fig. 19). Through the liquor folliculi run fine protoplasmic strands, which form a network, in the meshes of which are sparse granulosa cells. Owing to the formation of antrum folliculi, the position of the egg is shifted from the centre of the follicle to its periphery. The granulosa tissue has been differentiated into a basal layer of cells, which coat the basement membrane and, inside the latter, a confused layer of cells. Similarly, round the egg, granulosa cells have arranged themselves in a concentric layer nearest the oolemma, and outside the latter is an irregular layer of cells. With that the corona radiata has taken shape, but the germ hillock, the cumulus oophorus, or discus proligerus, is still unstalked. Owing to the incretion of follicular fluid, the follicle becomes distended and thus more spherical in shape.

During anestrus no normal vesicular follicles are met with, but they first make their appearance during pro-estrus and estrus. The formation of antrum folliculi will therefore probably be not only the prelude to the incretion of liquor folliculi but will also mark the beginning of the incretion of estrogen. The beginning of the vesicular phase, which almost coincides with the cessation of the increase in the size of the egg, therefore appears to indicate a physiological change in the activity of the granulosa cells.

Stage 8. In this stage, except for the release of the discus proligerus from the follicle wall, the granulosa layer attains its final shape. The layer which coats the basement membrane is columnar, with cell nuclei displaced towards the follicle vacuole, whereby a lighter zone appears against the basement membrane. Inside this layer there lies a confused layer of polygonal granulosa cells. Round the egg the granulosa cells have been differentiated in the same way, whereby a very beautiful corona radiata has been formed (fig. 25). The cumulus oophorus is clearly stalked, and similar vacuoles begin to appear in the stalk, as was the case in the formation of the antrum folliculi. The liquor folliculi now has a uniform structure, which, according to ROBINSON (1918),

VOL
28
194

is due to the incretion of the follicular liquor having changed character. That this is the case has been shown by SMITH (1937), who found that the osmotic pressure is increased, ROBINSON calls this follicular fluid "secondary liquor folliculi".

In the theca layer the externa has been further reinforced. The interna exhibits a very greatly developed vascular system, with strongly dilatated vessels. Here and there in these vessels there appear ruptures, and in certain cases the blood breaks through the basement membrane and the granulosa layer and leaks out into the antrum folliculi.

Stage 9. This stage begins immediately before ovulation and thus sees the fully developed follicle ready for ovulation (fig. 20). The stalk of the discus proligerus has disintegrated, and the egg, surrounded by the corona radiata and the outer confused granulosa layer, floats freely in the follicular liquor. The granulosa which coats the follicular wall exhibits increasing proliferative activity, with the result that it often has a wave-like appearance. This intensified cell division is, as far as can be judged, the prelude to the formation of the corpora lutea. In the theca layer three different zones can be distinguished, in that the theca interna now consists of an outer zone of loose connective tissue with polygonal cells interspersed in it, and an inner zone, which consists of a continuous layer of vessels nearest to the basement membrane. The ruptures in the vascular layer, through which blood leaks and penetrates into the basement membrane and the granulosa layer, are more usual in this stage than in the preceding one.

From each of these stages were selected 20 follicles, in stages 8 and 9, however, only 19 and 13 follicles respectively, in which the section passed through the centre of both the egg and the follicle. The longest and shortest axes of the follicle and egg respectively were then measured with an ocular-micrometer. In measuring the follicles the measurements were taken from the outer borderline of the theca externa and in measuring the eggs from the outer margin of the zona pellucida. After that the product of the long and short axes and its square root were computed. The square root values may be considered the approximate meandiameter of the eggs and the follicles respectively. The results of these measurements are presented in table 13 and fig. 21 and 22.

Table 13. *Mean diameter of ovum and follicle in relation to stage of follicle development.*

	Stage of follicle development								
	1	2	3	4	5	6	7	8	9
Number of follicles	20	20	20	20	20	20	20	19	13
Mean diameter of ovum in μ .	21.3	36.2	54.8	67.6	80.1	90.0	97.8	100.0	99.9
„ „ „ follicle in μ	22.9	42.8	71.3	117.0	191.6	276.9	532.9	901.8	1 072.4

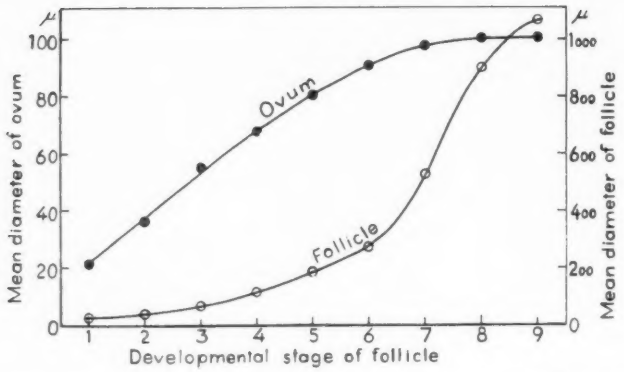


Fig. 21. Mean size of follicle and ovum at different follicle stages.

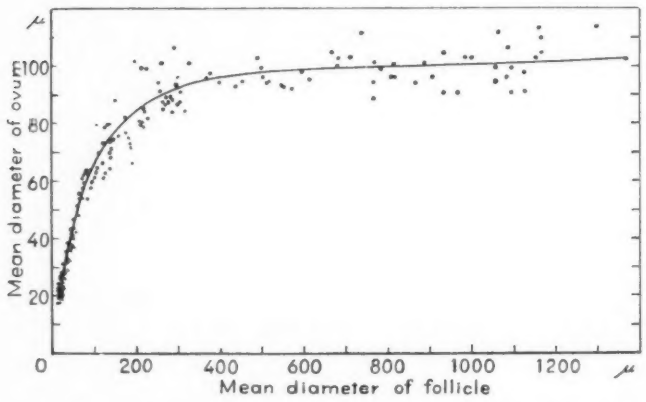


Fig. 22. Growth of the ovum in relation to the growth of the follicle.

From table 13 and fig. 21 it appears that the growth of the eggs take place at an earlier stage than that of the follicles. Up to the 6th—7th stage the egg grows very rapidly, but then the growth slows down and ceases entirely from the 8th stage. On the contrary the growth of the follicle is very slight during the first 6 stages but increases rapidly during the later ones. This circumstance appears still more clearly if the relation between the mean diameters of the egg and the follicle are studied irrespectively of the stages of development (fig. 22). From this it appears that on the whole the egg has completed its growth when the follicle has attained half its fullgrown size or when the approximate diameter has reached 500 μ.

The follicular development in mink thus shows no deviations from that in mice, guinea-pigs, rabbits, cats and ferrets (cf. Robinson 1918, Brambell 1928, Parkes 1931, Pincus 1936, Dempsey 1937, Pincus and Enzmann 1937, and Dawson and Friedgood 1940).

THE PHYSIOLOGY OF REPRODUCTION IN MINK

B. INFLUENCE OF MATING ON OVULATION.

Most of the animals examined, including man, have spontaneous ovulation, i.e. one which is independent of mating. According to HARTMAN (1939), in these cases mating appears to have no influence on the ovulation time. As opposed to this ovulation mechanism, there is the one where mating is a pre-condition for ovulation. This non-spontaneous ovulation has been proved in the ferret, the rabbit and the cat, the ground squirrel and the European weasel, cf. MARSHALL (1904), HEAPE (1905), LONGLEY (1911), FOSTER (1934) and DEANESLY (1944). PEARSON (1944) found that the same condition prevailed in the case of the short-tailed shrew. In this case, however, ovulation is not elicited unless the female is mated about twenty times during the course of a few days. Further, ALLEN (1922) found that certain mice ovulated spontaneously, while others had nonspontaneous ovulation. On account of the great variation in the length of the gestation period, the ovulation conditions for mink are of special interest, for this variation is caused either by differences in the interval between mating and fertilization (KELLER 1937), or by the lack of continuity in the embryonic development (PRELL 1930).

To throw light on the relation between ovulation and mating, autopsies were performed on 1. females in the estrus stage, 2. females which were isolated from males during the whole of the mating season, 3. females which were tried with males until they showed themselves willing to mate and were subsequently isolated from males during the remainder of the mating season, 4. females which were mated at different intervals before the autopsy, and 5. females which had been ridden by a male but not mated.

In order to ensure reliable control of the mating experiments, the vaginal smear was examined for sperms as soon as a female had been in close contact with a male. During the whole of the work more than 500 such controls were carried out. In no case was the keeper mistaken as to whether mating had taken place or not.

As in the case of the ferret (ROBINSON 1918), so also in the case of the mink it is difficult to decide by ocular inspection whether ovulation has taken place, especially when the ovulation rupture has had time to heal somewhat. In order to decide definitely whether ovulation had taken place, all the ovaries were fixed and sectioned in series, three sections in every millimetre being mounted. In the cases where the females had been mated, the interval from the mating to the autopsy was calculated from the commencement of the act of mating (table 14).

The four females which were autopsied during estrus, i.e. after they had shown readiness to mate, had not ovulated. Their ovaries contained numerous

Table 14. *Influence of mating on ovulation.*

No. of the female	Mating		Autopsy		Interval between mating and autopsy in hours	Ovulation	
	Date	Hour	Date	Hour			
15, 1940	—	—	21, 3	—	—	no ovulation	Unmated. Autopsy in estrus.
405, 1944	—	—	12, 3	—	—	,,	,, ,, ,, ,,
407, 1944	—	—	20, 3	—	—	,,	,, ,, ,, ,,
411, 1944	—	—	13, 3	—	—	,,	,, ,, ,, ,,
21, 1940	—	—	1, 4	—	—	,,	Isolated from male. Autopsy at the end of the mating season.
22, 1940	—	—	1, 4	—	—	,,	
20, 1940	—	—	30, 3	—	—	,,	Tested with male but not allowed to mate or play with the male. Autopsy at the end of the mating season.
23, 1940	—	—	1, 4	—	—	,,	
24, 1940	—	—	1, 4	—	—	,,	
1, 1941	5, 3	11,05′	6, 3	23,15′	36,10′	,,	Autopsied 36 hours after more than one hour's intimate sexual play with the male.
14, 1941	12, 3	9,00′	13, 3	21.30′	36,30′	ovulating	
18, 1941	13, 3	9,30′	14, 3	22,20′	36,50′	no ovulation	
2, 1940	15, 3	6,30′	15, 3	20,40′	14,10′	,,	Follicle growth activated.
414, 1944	11, 4	14,30′	12, 4	7,00′	16,30′	,,	,, ,, ,,
1, 1940	8, 3	14,15′	9, 3	15,00′	24,45′	,,	,, ,, ,,
7, 1940	7, 3	14,20′	8, 3	15,05′	24,45′	,,	,, ,, ,,
401, 1944	13, 3	9,00′	14, 3	13,05′	28,05′	,,	,, ,, ,,
5, 1941	8, 3	10,00′	9, 3	14,40′	28,40′	,,	,, ,, ,,
37, 1941	22, 3	9,20′	23, 3	14,00′	28 40′	,,	,, ,, ,,
408, 1944	22, 3	14,10′	23, 3	20,00′	29,50′	,,	,, ,, ,,
422, 1944	26, 3	14,15′	27, 3	21,10′	30,55′	,,	,, ,, ,,
402, 1944	13, 3	8,50′	14, 3	16,55′	32,05′	,,	,, ,, ,,
4, 1941	7, 3	10,10′	8, 3	22,15′	36,05′	,,	Ovulation immediately impending.
31, 1941	20, 3	9,15′	21, 3	21,45′	36.30′	ovulated	
45, 1941	26, 3	9,20′	27, 3	21,58′	36,38′	,,	

Females Nos. D_3, D_6, D_7, D_9, D_{10}, D_{12}, D_{13} and D_{15}, 1941 which were autopsied 37—39 hours after mating and females Nos. 4, 6 and 17, 1940 and 304, 306, 307 and 309, 1942 and 400, 403, 409, 413, 415, 417, 418, 420, 425, 426, 427, 432, 433 and 434, 1944, which were autopsied 42—50 hours after mating had all ovulated.

growing follicles. Only in a few cases were there follicles with stalked cumulus oophorus, and in no case had any follicle reached stage 8 as described in the preceding section.—This absence of fully developed follicles in mink during estrus conforms entirely with what ROBINSON (1918) found for ferrets.—One female, No. 407, 1944, exhibited onsetting follicular atresia in some follicles. On the other hand, the other females did not exhibit any follicular atresia, contrary to what is the case with polyestrous animals, such as mice, rats, guinea-pigs, etc.

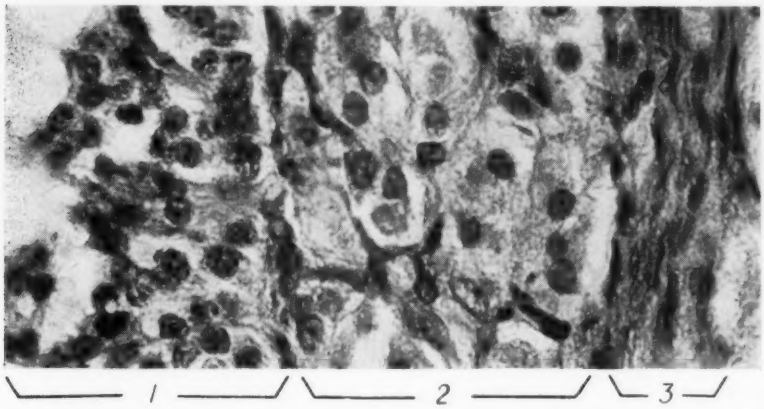


Fig. 23. Section through the wall of the follicle, showing theca interna luteinization. *1* granulosa, *2* theca interna, *3* theca externa. (Hemalun-eosin stained, redfilter, 600 ×.)

The two females which were entirely isolated from males and the three females which were tried with males until they showed themselves ready to mate, and which were then isolated during the remainder of the mating season, had not ovulated. The ovaries of these females had a unique appearance. They contained numerous fully developed follicles, with eggs floating freely in liquor folliculi. In the vasculosa of the theca interna vessels had ruptured, and blood had seeped out into the antrum folliculi. The granulosa had proliferated, so that it was wavy in appearance. Another peculiar feature was that many follicles in which the antrum folliculi had not yet been formed, contained eggs of fully developed size. In both these follicles and in the former ones the eggs exhibited degenerative features. The oolemma had begun to shrivel, and in some cases fragmentation of the protoplasm could be observed. In the follicles where the antrum folliculi had not yet been formed, apart from changes in the egg, only changes in the granulosa could be found, vacuoles being met with in it, and the cell nuclei being small and strongly stainable. With the exception of the increase in the size of the eggs, the changes in these follicles completely corresponded to the obliteration atresia which KOVÁCS (1933) found in the primary follicles of dogs. In the above-described, fully developed follicles a regressive and a progressive process could be distinguished. Apart from the degeneration of the egg, the regressive process also involved the granulosa layer. Especially towards the border-line of the antrum folliculi, cells with small, strongly stainable nuclei were met with, and in certain cases entirely free cell nuclei. The progressive process was met with in the theca interna, where the originally polygonal cells had proliferated and formed so-called theca lutein cells, which appeared completely to correspond to the cells in the interstitial glandular tissue to which they certainly belong (fig. 23). On account of the proliferation in the theca interna, the granulosa layer of the follicles

had penetrated into the antrum folliculi. These follicles seem to correspond in all respects to the cystic follicles observed in ferrets by ROBINSON (1918), and which PINCUS and ENZMANN (1937) found in rabbits, KOVÁCS (1933) in dogs, and GREULICH (1934) in cats.

The circumstance that the females autopsied during estrus and after the end of the mating season had not ovulated indicates that ovulation is dependent on mating. For the purpose of studying this interplay more closely autopsies were made at different intervals after the matings.

Two females, which were autopsied 14 and 17 hours respectively after copulation, exhibited strongly activated follicular growth. In the most developed follicles the cumulus oophorus was stalked, and ruptures in the blood capillaries of the theca interna had begun to appear. The liquor folliculi had changed its character and corresponded to the secondary liquor folliculi described by ROBINSON (1918). As SMITH (1937) showed, this change implies also a greatly increased osmotic pressure. The fact that follicular growth is so rapidly activated after mating indicates that the nerval stimulation which copulation exercises on the hypophysis almost immediately leads to incretion of substances which stimulate the development of the follicles.

Two females which were autopsied 24 h. 45 m. after mating had follicles which had almost reached stage 9, described in the preceding section. The only difference which these follicles exhibited, as against follicles ready for ovulation, was that the granulosa layer had not yet begun to proliferate as a preliminary to the formation of the corpus luteum.

Four females which were autopsied 28 h. 5 m.—29 h. 50 m. after mating, and two females which were autopsied 30 h. 55 m.—32 h. 5 m. after mating, all had strongly developed follicles. In these females the granulosa had begun to proliferate (fig. 24). In several cases, owing to ruptures in the vasculosa of the theca interna, blood had seeped out into the antrum folliculi. In these stages the follicle appears like a blunted cone on the surface of the ovary. As appears from fig. 10 the ovulation stigma appears as a light avascular spot, around which dilatated vessels can be observed. The ovulation stigma in mink appears closely to conform to the corresponding formation in rabbits (WALTON and HAMMOND 1928, MARKEE and HINSEY 1936 and HILL, ALLEN and KRAMER 1935).

Female No. 4, 1941, which was autopsied 36 h. 5 m. after mating, had not ovulated, but ovulation appeared to be imminent, for the proliferation in the granulosa was enormous. The two females autopsied 36 h. 30 m. and 36 h. 38 m. after mating, as also the 8 females autopsied 37—39 hours after mating and 21 females autopsied 42—50 hours after mating, had all ovulated.

If the results of these examinations are summarized, it is found that the females did not ovulate if they were isolated from males or were not

VOL
28
194

allowed to mate. If the females mate the follicles grow rapidly, and ovulation follows 36—37 hours afterwards. Therefore it may be considered proved that the ovulation of the female mink is dependent on mating, as is the case with the ferret, the rabbit, the cat, the ground squirrel, the weasel, and the shrew, and thus, too, the explanation of the great variation in the length of the gestation period in the mink advanced by KELLER (1937) proves to be incorrect.

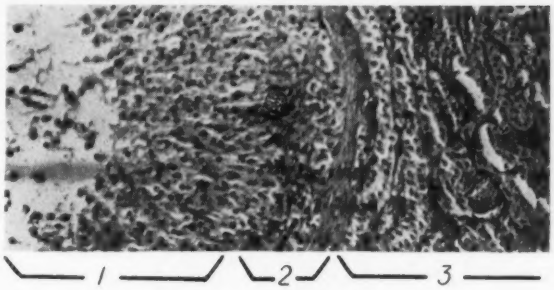


Fig. 24. Section through the wall of the follicle immediately before ovulation. *1* granulosa, *2* theca, *3* cortex tissue. (Hemalun-eosin stained, redfilter, 100 ×.)

During the year 1940, when preliminary investigations of the ovulation mechanism were being carried out, some females which had not permitted mating were sent in by a mink farmer. A scrutiny of the ovaries showed that one of these females had fully developed corpora lutea, which means that she had ovulated. As the female rabbit ovulates if she is mounted by a male or even by another female, it was considered possible that the same might be true of the mink female. With the object of investigating this more closely, a male with pronounced copulative impotence was allowed to mount three females for at least one hour, and autopsy was performed 36 h. 10 m.—36 h. 50 m. after the mounting had begun. All three females exhibited follicles ready for ovulation, and one female had two ruptured follicles. The ovulation of the other females was immediately impending. Thus the mounting by the male, without actual mating, had elicited ovulation. In the further investigations all the males which exhibited a tendency to mount females, without mating, were weeded out. In spite of this precautionary measure, in the total material, comprising about 300 matings, a further 11 cases were met with where mounting by males had elicited ovulation. From this it may be concluded that, in practical mink breeding, the frequency of such ovulations must be great, and as in many cases they may lead to the non-occurrence of gestation, they constitute a serious problem.

Further, in the total material 4 cases were met with where the females did not ovulate after mating. One of these females No. 305, 1942, was mated twice, but did not ovulate. The female's ovaries exhibited a completely inactive picture, and therefore it is probable that she was in such a sexual condition that she could not be stimulated to ovulation at all. In the other three cases the copulation was short, 5—23 mins., and therefore it is possible that it was not sufficiently intensive to start the ovulation mechanism.

C. INFLUENCE OF RE-MATING ON OVULATION.

It was shown above that mating elicits ovulation. In this case, however, only the first mating during the mating season has been studied. In section III it was shown that, during one and the same mating season, the female mink permits several matings at irregular intervals. The question then presents itself whether re-matings also elicit ovulation. After mating, rabbits, ferrets and cats, which also have non-spontaneous ovulation, pass into a stage of pregnancy or pseudo-pregnancy of varying length, and in rabbits, and certainly also in ferrets and cats during that time, a fresh mating does not elicit ovulation (HAMMOND and MARSHALL 1925).

For the purpose of investigating whether the female mink ovulates more than once during the mating season, and, if such is the case, whether a certain time must elapse between the matings for a fresh ovulation to take place, females were mated twice at varying intervals, autopsies being performed 37—50 hours after the second mating. The ovaries of all the females were sectioned in series, in order to decide whether ovulation had taken place at both matings and to determine the number of ovulated follicles. At the same time, the uterine tubes and uterus were examined in respect of the occurrence of embryos. In 13 cases this was done by means of sections, and in other cases by massaging the uterine tubes and flushing out the uterus.

40 females were included in the investigations, and the results are very convincing (table 15). The only exceptions are female No. 305, 1942, which did not ovulate after any mating, and female No. 400, 1944, which did not ovulate after the first mating. The cause of this has been discussed in the preceding section. The experimental data for the other females may be summarized as follows: Females which are re-mated at intervals of 1—4 days do not ovulate after the second mating. Females which are re-mated at intervals of 5—6 days sometimes ovulate after the second mating also. Females which are re-mated at longer intervals than 6 days always ovulate after the second mating. These results show that there is a definite refractory period in the mechanism of ovulation. Further that after the end of this period mating elicits ovulation, contrary to conditions with the rabbit, the cat and the ferret.

That a certain time must elapse between the matings for a fresh ovulation to be possible may be due to different causes. As is shown in section VII, the corpora lutea are quite inactive during this refractory period, and therefore this period cannot be explained on the assumption that the incretion of progesterone suppresses the release of hormones from the anterior pituitary. In connection with studies of implantation (see page 106) it was found that injections of extracts of pregnancy urine (P. U.) and pregnancy mare serum (P. M. S.) do not elicit ovulation during the refractory stage. This together

Table 15. *Influence of re-mating on ovulation.*

No. of the female	Date of		Interval between first and second mating in days	Number of ovulated follicles after			
				First mating		Second mating	
	First mating	Second mating		Ovary A	Ovary B	Ovary A	Ovary B
312, 1942	9, 4	10, 4	1	3	4	0	0
D_1, 1941	4, 3	6, 3	2	3	4	0	0
D_2, 1941	4, 3	6, 3	2	2	4	0	0
300, 1942	13, 3	15, 3	2	3	8	0	0
302, 1942	13, 3	16, 3	3	3	3	0	0
D_4, 1941	5, 3	9, 3	4	3	4	0	0
301, 1942	11, 3	15, 3	4	3	5	0	0
303, 1942	11, 3	16, 3	5	5	6	0	0
305, 1942	16, 3	21, 3	5	0	0	0	0
410, 1944	11, 3	16, 3	5	4	7	0	0
415, 1944	11, 3	16, 3	5	4	5	1	4
D_5, 1941	5, 3	11, 3	6	2	5	[1]	[1]
404, 1944	15, 3	21, 3	6	3	5	0	0
431, 1944	20, 3	26, 3	6	5	8	0	0
403, 1944	10, 3	16, 3	6	4	2	4	2
427, 1944	18, 3	24, 3	6	7	3	4	3
306, 1942	16, 3	23, 3	7	0	3	1	4
418, 1944	17, 3	24, 3	7	3	1	8	4
425, 1944	19, 3	26, 3	7	1	8	3	6
D_3, 1941	4, 3	12, 3	8	0	5	1	3
D_6, 1941	4, 3	12, 3	8	3	3	2	2
304, 1944	11, 3	19, 3	8	5	5	5	2
413, 1944	9, 3	17, 3	8	4	4	2	3
308, 1942	22, 3	31, 3	9	1	7	1	6
420, 1944	15, 3	24, 3	9	4	3	5	4
433, 1944	18, 3	27, 3	9	1	2	3	1
434, 1944	20, 3	29, 3	9	2	5	1	4
426, 1944	16, 3	26, 3	10	3	4	5	2
D_7, 1941	4, 3	15, 3	11	6	0	3	4
D_{15}, 1941	4, 3	15, 3	11	7	1	4	3
307, 1942	15, 3	26, 3	11	2	6	2	4
400, 1944	27, 3	7, 4	11	0	0	1	4
432, 1944	25, 3	5, 4	11	3	4	2	5
409, 1944	9, 3	22, 3	13	5	4	4	3
417, 1944	23, 3	5, 4	13	12	1	4	4
D_8, 1941	4, 3	18, 3	14	4	4	(2)[1]	(8)[1]
D_{10}, 1941	4, 3	18, 3	14	4	5	5	4
D_9, 1941	4, 3	24, 3	20	12	3	1	5
D_{12}, 1941	4, 3	24, 3	20	4	5	6	5
D_{13}, 1941	4, 3	1, 4	28	1	4	3	3

[1] The female just ovulating after the second mating.

with the fact that injections of P. U. (cf. HILL and PARKES 1931) cause ovulation in hypophysectomized rabbits, indicates that the refractory period cannot be explained on the assumption that the anterior pituitary requires a certain time for recovery between the incretion phases of ovulation-eliciting substances. In this connection it is of interest to note that BURDICK and CIAMPA (1944) found that in mice the injection of P. M. S. regularly causes ovulation during pregnancy. When such injections are made during the first three days after ovulation, however, ovulation very seldom occurs. When these possibilities of explaining the refractory period in mink are eliminated there remains only one, namely that during the refractory stage there are no such follicles in the ovaries as can be stimulated to ovulate. This interpretation is supported by the fact that both the number of ovulating follicles and the number of cubs born increase with an increasing length of the interval between matings (table 16 and 41). Of course, this interpretation does not eliminate the possibilities that the anterior pituitary also requires a certain time for recovery.

That the mink female ovulates again if re-mated after the end of the refractory stage is due to the fact that she returns to an estrous stage after ovulation, the reason for this being an inactive stage in the development of corpora lutea (see page 84).

At many mink farms the females have been mated only once during the mating season, with satisfactory results on the whole. In the present writer's investigations, too, it proved that, as a rule, the females become pregnant after only one mating. It is then a question of very great interest what happens to the fertilized eggs which, in the majority of cases, must still be in the uterine tubes or uterus at the time of the second mating. Out of 27 females which ovulated twice, fertilized eggs from the first ovulation could be found in only two cases. Thus as a rule, the eggs from the first ovulation perish in connection with the second mating and ovulation. That the mating in itself does not lead to the destruction of the eggs appears from the fact that the females which had not ovulated after the second mating all had fertilized eggs in the uterine tubes. As no dead eggs from the first ovulation could be found in the uterine tubes or uterus of the females which ovulated twice, it would seem that the eggs must have been ejected through the cervix in connection with the second ovulation.

As mentioned above, in two cases fertilized eggs from the first ovulation were found. The female No. D_5, 1941, thus had 8 to 16-celled eggs in the uterine tubes immediately before the second ovulation and the female No. 308, 1942, had one blastula in the uterus after the first ovulation, at the same time as there were fertilized 2-celled eggs in the tubae from the second ovulation. In the first-mentioned case it is uncertain whether the eggs from the first ovulation would also have remained after the second ovulation. On the other hand,

the last-mentioned case indicates that superfetation may occur in mink. It is of interest in this connection that KELLER (1944) describes two cases of superfetation in mink. In one case a female died immediately after having given birth to normally developed foetuses. In an examination of the uterus, foetuses estimated to be 14 days younger than those born were found. In the second case a female gave birth to two normal litters with an interval of 8 days. A Swedish breeder, KINCK, reported, in the year 1945, that on his farm a female gave birth to 6 normally developed young and 4 which appeared to be half-term. As BUCHANAN—SMITH (1927), AUBEL (1932), SWINEHART (1939), SCHÜTZE (1940) and LITTLEFORD and GYSIN (1944) considered that they could prove superfetation in sheep, pigs and mice, and as SNYDER and WISLOCKI (1931) experimentally obtained superfetation in rabbits, it appears to be established that superfetation also occurs in mink. However, this phenomenon will hardly be of any practical importance for mink breeding.

Thus, by way of summary, it may be said that the female mink may ovulate even after re-mating, if the interval from the previous mating is at least 5 or 6 days. As a rule re-mating leads to the destruction of the foetuses from the previous mating. The reason why females permit re-mating, in spite of the presence of fertilized eggs from the previous mating in the tuba or uterus, appears to be that the corpora lutea are inactive.

D. FACTORS CONTROLLING THE NUMBER OF RUPTURING FOLLICLES.

The fact that there is a refractory period in the mechanism of ovulation makes it of interest to investigate how the interval between the matings affects the number of rupturing follicles at the second ovulation. Therefore those females in table 15 which ovulated after both matings have been collocated in table 16, the number of rupturing follicles at the first ovulation also being given. Owing to the small number of females, the average number of ruptured follicles varies greatly, though there is a slight tendency towards an increase in the number with longer intervals between the matings. As the individual differences in the females may give rise to differences in the average values for the groups, the number of ruptured follicles after the second mating has also been calculated as a percentage of the number of ruptured follicles after the first mating. These percentage figures indicate a slight tendency towards an optimum in the number of rupturing follicles 7—10 days after a previous ovulation.

As appears from the total average values, the number of ruptured follicles at the first mating was 7.6 and at the second 6.8. This decline may be due to random variation but may also be due to the shortness of the time of follicular development.

Table 16. *Influence of the interval between matings on the number of ovulated follicles in the second ovulation.*

Interval between matings in days	Number of females	Mean number of ovulated follicles after		
		First mating	Second mating	Second mating as a percentage of first mating
5— 6	3	8.3	6.0	72
7— 8	7	6.5	6.6	102
9—10	5	6.4	6.4	100
11—12	4	7.3	6.5	89
13—	6	10.0	7.8	78
Total	25	7.6	6.8	89

A question of great importance is how the number of rupturing follicles are checked. ASDELL (1924) found that, if unilateral ovariectomy was performed, the intact ovary tended to develop as many follicles as both the ovaries together had done previously. WALTON and HAMMOND (1928) showed that the number of ovulated eggs in rabbits varied greatly in the different breeds, but showed striking constancy within one and the same breed. They also found that if the fully-developed follicles in an ovary were destroyed, new follicles appeared immediately, so that there was always a constant number of fully-developed follicles in the ovaries. These results indicate a tendency in the ovaries to ovulate a certain fixed total number of follicles.

In an endeavour to elucidate this problem further, an analysis of variance was made. This analysis comprises the females in table 15, which ovulated twice. Owing to the fact that the number of ovulated follicles was determined for separate ovulations in each ovary, it was possible to group the variation according to the several causes, including the primary non-linear interactions (table 17). In this connection only a few of these causes are of interest. Firstly the mean square corresponding to differences between means of females as compared with the error mean square does not indicate any differences between the females as regards the number of ovulated follicles. Further the ratio of the mean square of the non-linear interactions between females and ovaries and the error mean square shows no significance. On the other hand the ratio of the error mean square and the mean square of the non-linear interactions between females and ovulations indicates a negative intra-class correlation. This negative intra-class correlation must be interpreted in the sense that each ovary tends to ovulate such a number of follicles that the total of ovulated follicles in the two ovaries is as constant as possible in different ovulations. When the ratio of the mean square of the non-linear interactions between females and ovaries and the mean square of the non-linear interactions between females and ovulations is calculated, a highly significant value is

Table 17. *Analysis of variance of the number of ovulated follicles in each separate ovary during different ovulations.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Ratios of mean squares
Between females	24	84.54	3.523	$\frac{7.687}{4.771} = 1.61$
Between ovaries	1	0.25	0.250	
Between ovulations	1	4.41	4.410	$\frac{4.771}{2.389} = 2.00^{*}$
Primary non-linear interactions:				
females—ovaries	24	184.50	7.687	$\frac{7.687}{2.389} = 3.22^{**}(*)$
females—ovulations	24	57.34	2.389	
ovaries—ovulations	1	2.25	2.250	
Secondary non-linear interactions and random variation (error)	24	114.50	4.771	
Total	99	447.79	4.523	

obtained. The only possible explanation of this difference is either a tendency in each ovary to repeat the number of ruptured follicles in different ovulations, or a compensatory effect in ovulation, the ovaries tending to ovulate a certain fixed total of follicles. Thus the analysis entirely verifies the experimental results obtained by ASDELL (1924) and WALTON and HAMMOND (1928).

The fact that, not the separate ovaries, but the two ovaries together, tend to ovulate a constant number of follicles from ovulation to ovulation shows that the mechanism which regulates the number of ovulated follicles is not isolated to the individual ovary, for this mechanism must be capable of co-ordinating the ovulation of the ovaries. DAHLBERG and ÅKESSON (1930) advanced the explanation that as a rule only one egg is released in ovulation in Man because a maturing ovum secretes a hypothetical substance, ovein, which stimulates surrounding cells to secrete an ovulating-inhibiting hormone. This hormone was assumed to be identical with estrogen. Later investigations have shown that the incretion of estrogen is not regulated by the maturing ovum, but by the anterior pituitary gland by means of co-operation of the follicle-stimulating (FSH) and the luteinizing (LH) factor (cf. FEVOLD 1941, and ASTWOOD 1941). On the other hand, the fact that estrogen actually inhibits the release of the follicle-stimulating hormone from the anterior pituitary has been verified by several workers (cf. WITSCHI and PFEIFFER 1935, DEMPSEY 1937, FEVOLD 1939 a, b, MERCKEL and NELSON 1940, ASTWOOD 1941 and others). The circumstance that every animal species tends to ovulate a definite number of eggs at each ovulation may be explained on the assumption that estrogen incretion regulates the incretion of follicle-stimulating hormone from the hypophysis. It is then presumed that the release of follicle-stimulating hormone from the anterior pituitary can only continue until the amount of estrogen

in the blood has reached a certain value. When that stage is reached, the release of FSH is arrested, so that only a limited number of follicles can develop. That the ovaries themselves do not determine the number of rupturing follicles is shown by the fact that the number of rupturing follicles can be violently increased by the injection of FSH (cf. WISLOCKI and GOODMAN 1934, PINCUS 1940, and HAMMOND and BHATTACHARYA 1944).

That different animal species ovulate different numbers of eggs can be explained, on the assumption that the incretion of estrogen in a follicle in relation to the incretion of follicle-stimulating hormone (FSH) is in inverse proportion to the number of rupturing follicles. On the other hand, this circumstance can also be explained on the assumption that there are different positions of equilibrium for the incretion of estrogen and FSH in different animals, but the correctness of such an assumption appears to be none too probable.

VI. VARIATIONS IN THE RATE OF EMBRYONIC DEVELOPMENT.

As ovulation in mink takes place at a definite interval of time after mating, and as, in all the animals examined, the unfertilized eggs, without exception, have a very short life after ovulation (cf. LONG 1912, HAMMOND 1934, HAMMOND and WALTON 1934 a, MYERS, YOUNG and DEMPSEY 1936, and HARTMAN 1939), the initiation of embryonic development in mink must bear a very constant relation to the time of mating. Therefore the variations in the length of the gestation period cannot be due to there being different intervals from mating to fertilization, as KELLER (1937), assumed. Unless the rate of embryonic development varies from female to female, there remains only one possible explanation of this gestation variation, namely that at parturition the foetuses have reached different stages of development. As has been shown in a series of investigations (cf. TEEL 1936, NELSON, PFIFFNER and HATERIUS 1930, HAIN 1932, 1934, SNYDER 1934, 1938, HOOPER and KING 1935, HECKEL and ALLEN 1937, KING 1938, and others), the foetuses of rabbits and rats invariably die if parturition is delayed a few days beyond the normal time. It does not appear probable, therefore, that the foetuses are born at different stages of development. Nor can any degree of development in the young which is correlated with the length of gestation be proved at parturition. This simplifies the problem. The variation in the length of gestation must in consequence be due to a corresponding variation in the rate of embryonic development.

In an attempt to throw light on this question, autopsies were performed at different intervals after mating. In order to solve the problem, it was necessary

to try, firstly, to obtain as large a total variation in the rate of embryonic development as possible, and secondly to obtain as large a variation as possible in the rate of embryonic development in the females which were autopsied at the same intervals after mating. As was shown in section III, the length of the gestation period decreases when the date of mating is moved forward. With this observation as a starting point, the females which were to be autopsied at the same interval after mating were grouped in such a way that the variation in their mating dates was as large as possible. In carrying out the investigations, special precautionary measures were taken in the mating experiments. Special keepers carefully watched every attempt at mating, and as soon as the females had been in close contact with the males, specimens of the vaginal smear were taken, to control whether mating had or had not taken place. As soon as a female had mated, she was transferred to a special department, in order to eliminate every possibility of mistake. At autopsies the rule was followed, practically without exception, that one uterine horn with its appurtenant tuba was used for post-examinations of embryos in vitro, while the other uterine horn, with its tuba and the ovaries and vagina, were fixed for histological examination. In order to be able to compare blastulae and implanted foetuses respectively from different females at the same time, photographs of them were taken.

OL.
28
947

These investigations comprised 56 females. Owing to non-mating and non-fertilization and to total resorption and deaths of foetuses, the number of females which had living embryos at autopsy was reduced to 38. During the year 1941 twenty-four females which had been mated were received from a breeder who gave up his farm at the end of the mating season. These females were all killed on 7th April. One of them had had only one mating during the mating season, and this female was therefore put together with the 38 females mentioned above. Ten females had mated twice, with at least 8 days between the matings, but two of them proved not to have such a large number of corpora lutea in the ovaries that it could be assumed with certainty that they had ovulated twice. These two females and the other 13 in the case of which it could not be decided with certainty which mating had resulted in fertilization, were entirely excluded from the investigation. The 8 females which had been mated twice, with at least an 8-day interval, were in reality a very valuable complement to the once-mated females. The latter were tried with males until they accepted mating. That implies that as a rule they were mated at the beginning of estrus. On the other hand, the re-mated females became pregnant after a mating which took place at least 8 days after the beginning of estrus. The two materials may therefore throw light on the important question as to whether the length of the gestation period is affected if the female is mated at the beginning of estrus or later. The objections may be raised against the re-mated females, firstly that they had not been under

Table 18. *Variation in the rate of the embryonic development. Once-mated females.*

No. of the female	Date of		Interval between mating and autopsy in days	Number of corpora lutea	
	Mating	Autopsy			
3, 1940	17, 3	20, 3	3	4+11	Ova with 4 blastomeres in tuba uterina
23, 1941	15, 3	18, 3	3	3+ 6	„ „ 2—4 „ „ „ „
27, 1941	18, 3	21, 3	3	3+ 4	„ „ 2—4 „ „ „ „
D_1, 1941	4, 3	7, 3	$3\frac{1}{2}$	3+ 4	„ „ 4 „ „ „ „
D_2, 1941	4, 3	7, 3	$3\frac{1}{2}$	2+ 4	„ „ 4 „ „ „ „
300, 1942	13, 3	17, 3	4	3+ 8	„ „ 4—8 „ „ „ „
21, 1941	14, 3	19, 3	5	2+ 4	„ „ 8—16 „ „ „ „
34, 1941	20, 3	25, 3	5	7+ 9	„ „ 8—16 „ „ „ „
D_4, 1941	5, 3	11, 3	6	3+ 4	„ „ 8—16 „ „ „ „
301, 1942	11, 3	17, 3	6	3+ 5	„ „ 8—16 „ „ „ „
303, 1942	11, 3	18, 3	7	5+ 6	„ „ 8—32 „ „ „ „
29, 1941	19, 3	27, 3	8	2+ 5	Blastula in uterus
41, 1941	22, 3	30, 3	8	4+ 6	„ „ tuba uterina
D_5, 1941	5, 3	13, 3	8	2+ 5	„ „ „ „
14, 1940	12, 3	21, 3	9	2+ 4	„ „ uterus
9, 1940	3, 4	13, 4	10	6+ 6	„ „ „
10, 1940	16, 3	26, 3	10	5+ 8	„ „ „
11, 1940	10, 3	20, 3	10	4+ 4	„ „ „
309, 1942	31, 3	11, 4	11	4+ 7	„ „ „
12, 1941	11, 3	23, 3	12	3+ 4	„ „ „
30, 1941	19, 3	31, 3	12	3+ 8	„ „ „
42, 1941	22, 3	3, 4	12	6+ 7	„ „ „
26, 1941	17, 3	2, 4	16	3+11	Blastula implantating
36, 1941	20, 3	5, 4	16	5+ 8	„ in uterus
40, 1941	22, 3	7, 4	16	4+ 4	„ „ „
24, 1941	15, 3	4, 4	20	2+10	„ „ „
32, 1941	20, 3	9, 4	20	3+ 4	„ „ „
35, 1941	20, 3	9, 4	20	5+ 8	„ implantating
311, 1942	20, 3	11, 4	22	3+ 4	„ „
9, 1941	9, 3	3, 4	25	2+ 6	„ in uterus
39, 1941	22, 3	16, 4	25	6+ 6	„ implanted
103, 1941	9, 3	7, 4	29	7+ 9	2+4 implanted embryos
8, 1941	9, 3	8, 4	30	5+ 6	2+4 „ „
33, 1941	20, 3	19, 4	30	2+ 7	„ „
38, 1941	22, 3	21, 4	30	4+ 7	4+/5/6 „ „[1]
43, 1941	24, 3	23, 4	30	2+ ?	4+5 „ „
44, 1941	24, 3	28, 4	35	5+ 9	4+5 „ „
3, 1941	6, 3	15, 4	40	7+ 7	1+2 „ „
16, 1941	12, 3	21, 4	40	? ?	2+2 „ „

[1] In one implantation site monozygous twins.

VOL
28
194

sharp control, and secondly that the occurrence of superfetation may complicate the results. In reply to the first objection, it may be pointed out that the owner gave very exact information about matings and tests, and that the females were carefully watched during the mating season. Nor were there any signs of superfetation in the material.

The results from the once-mated females have been collocated in table 18, and those from the twice-mated females in table 19. It has not been possible to reproduce photographs of the embryos from all the 47 females, nor was it considered necessary, for at autopsy several females had foetuses at almost the same stage of development. Instead, a series of embryos at different stages of development have been collocated in figs. 25—47. This series will afford guidance in the following description of the rate of embryonic development in mink.

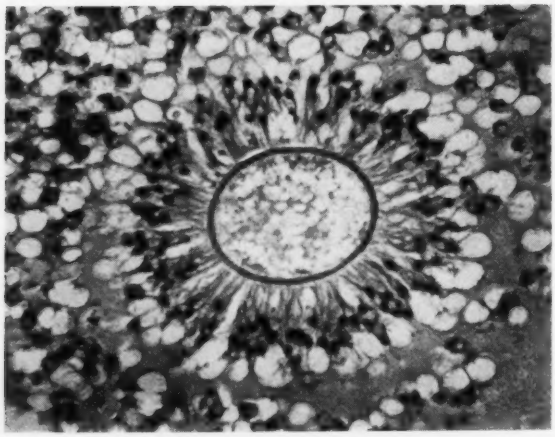
In the follicle which is ready for ovulation the egg floats freely in liquor folliculi and is surrounded by an extremely beautiful corona radiata, (fig. 25). At ovulation the egg is released, still surrounded by the corona radiata and accompanied by granulosa cells, mainly originating from the dissolved cumulus oophorus. Fig. 26 shows two newly ovulated eggs found in the infundibulum. As a rule the egg is freed from the corona radiata already in the infundibulum, which implies that fertilization takes place there.

The passage of the egg through the first half of the tuba is very rapid, as is the case with other animals (cf. BISCHOFF 1844, ROBINSON 1918, WESTMAN 1926, ANDERSEN 1927, ALDEN 1942, and others). 48 hours after the mating of mink, i.e. 12 hours after ovulation, the eggs were found in the middle part of

Table 19. *Variation in the rate of the embryonic development. Females re-mated after an interval of at least 8 days.*

No. of the female	Date of first mating	Date of second mating	Date of autopsy	Interval between second mating and autopsy	Number of corpora lutea		
105, 1941	6, 3	18, 3	7, 4	20	9 + 10	4 + (6) 7	implanted embryos[1]
93, 1941	9, 3	17, 3	7, 4	21	6 + 11	3 + 6	,,
109, 1941	6, 3	17, 3	7, 4	21	8 + 10	4 + 4	,,
98, 1941	8, 3	16, 3	7, 4	22	8 + 9	3 + 4	,,
107, 1941	8, 3	16, 3	7, 4	22	7 + 10	2 + 5	,,
97, 1941	5, 3	14, 3	7, 4	24	9 + 10	6 + 6	,,
95, 1941	5, 3	13, 3	7, 4	25	8 + 10	2 + 3	,,
104, 1941	4, 3	13, 3	7, 4	25	3 + 10	4 + 4	,,

[1] In one implantation site monozygous twins.



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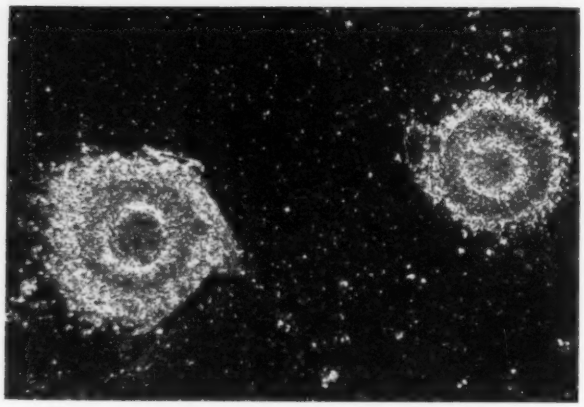

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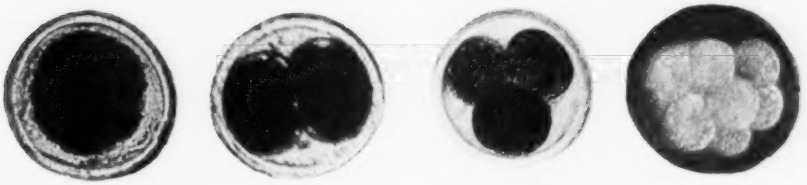
Figs. 25—26. — 25. Section through the ovum with corona radiata in a follicle almost ready to ovulate. (Hemalun-eosin stained, greenfilter, 225 ×.) — 26. Two ova, which were found in the mouth of the infundibulum immediately after ovulation. The ova are still surrounded by the cumulus oophorus and thus not yet fertilized. (90 ×.)

Figs. 27—39. — 27. Fertilized ovum, which is just commencing the first cleavage. The ovum was found in the middle part of the tuba, 12 hours after ovulation. (180 ×.) — 28. Fertilized ovum with two blastomeres. The ovum was found in the middle part of the tuba, 25 hours after ovulation. (180 ×.) — 29. Fertilized ovum with four blastomeres. The ovum was found in the isthmus of the tuba, 36 hours after ovulation. (180 ×.) — 30. Fertilized ovum with eight blastomeres. The ovum was found in the isthmus of the tuba, 84 hours after ovulation. (180 ×.) — 31. Morula, found in the tubo-uterine part of the tuba, 6 1/2 days after ovulation. (180 ×.) — 32. Blastula, found in the tubo-uterine part of the tuba, 6 1/2 days after ovulation. (180 ×.) — 33. Blastula, found in the uterus of female No. 30, 1941, 12 days after mating. (90 ×.) — 34—35. Blastulae found in the uterus of female No. 12, 1941, 12 days after mating. (90 ×.) — 36. Blastula found in the uterus of female No. 42, 1941, 12 days after mating. (90 ×.) — 37. Blastula found in the uterus of female No. 40, 1941, 16 days after mating. (90 ×.) — 38. Blastula found in the uterus of female No. 26, 1941, 16 days after mating. (90 ×.) — 39. Blastula found in the uterus of female No. 24, 1941, 20 days after mating. (45 ×.)



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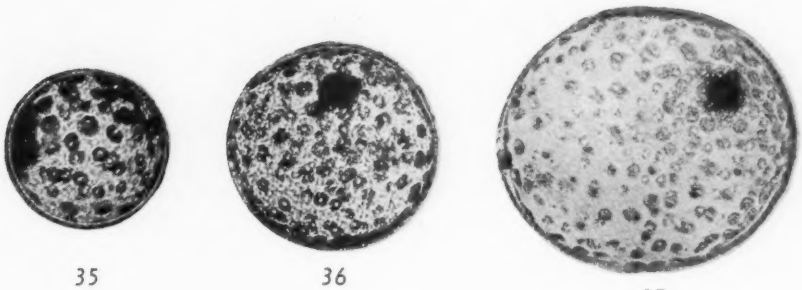

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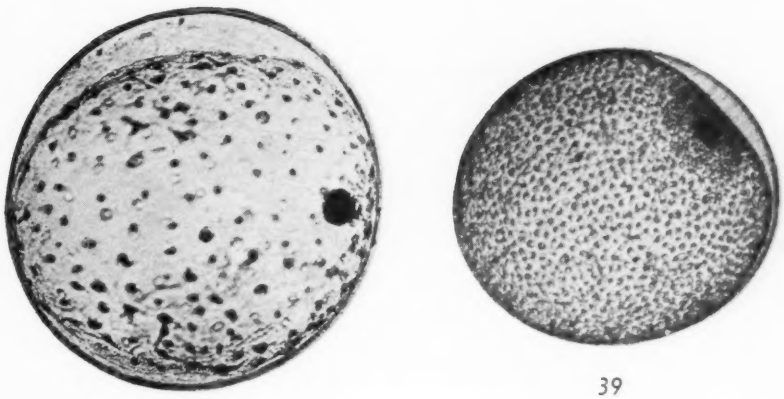

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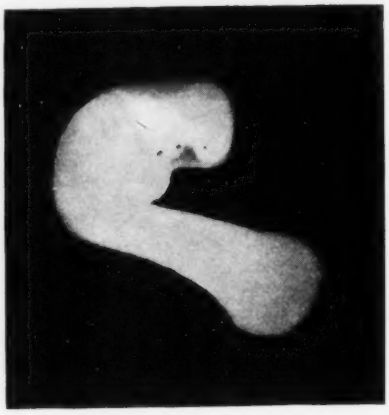
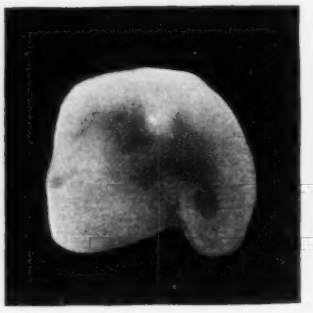


41

VOL
28
194



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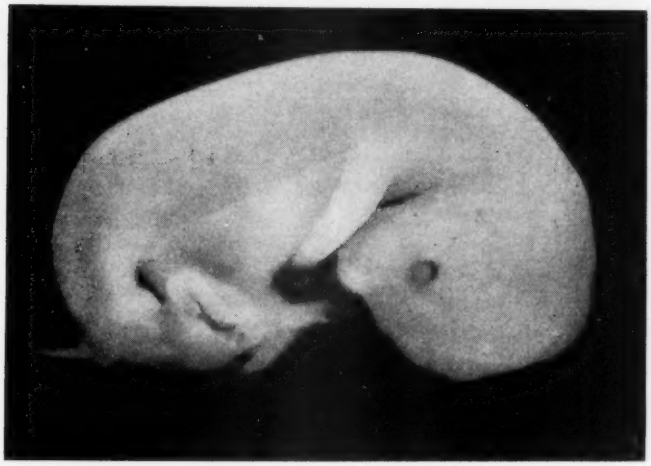

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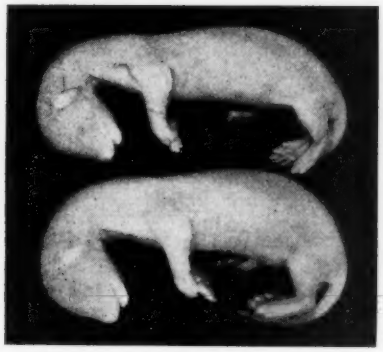

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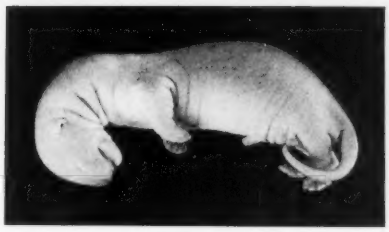


47

Figs. 45—47. — 45. Embryo from female No. 44, 1941, 35 days after mating. (6 ×.) — 46. Embryo from female No. 16, 1941, 40 days after mating. (1.0 ×.) — 47. The embryonal development at partus. (0.8 ×.)

Figs. 40—44. — 40. Embryo from female No. 33, 1941, 30 days after mating. Note the yolk sac and the differentiation into somites. (37.5 ×.) — 41. Embryo from female No. 98, 1941, 22 days after mating. (22.5 ×.) — 42. Embryo from female No. 105, 1941, 20 days after mating. (6 ×.) — 43. Embryo from female No. 95, 1941, 25 days after mating. (6 ×.) — 44. Embryo from female No. 3, 1941, 40 days after mating. (6 ×.)

the tuba. At that point of time the eggs are generally unicellular (fig. 27). During their further passage through the tuba, cell cleavage continues, so that the blastula stage has been reached when the fertilized eggs pass down into the uterus. In figs. 27—32 are shown fertilized eggs from the tuba at different stages of development.

Eight days after mating, the blastodermic vesicles were found in the tuba in two cases and in the uterus in one case, see table 18. After that time the blastodermic vesicles were found in the uterus in all cases. This shows that the passage of the eggs through the tuba takes 6—7 days. Thus, as the passage through the first half of the tuba takes only about 12 hours, the passage through the second half takes place very slowly, or at an average rate of about 0.04 mm per hour. Without entering upon any discussion of the various theories as to egg transport advanced by different research workers, which have been reviewed by WESTMAN (1926), HARTMAN (1932), and ALDEN (1942), it must be pointed out that, at any rate with mink, it appears to be difficult to explain the slow passage through the latter half of the tuba either by the ciliar or by the muscular theory. On the other hand, it can be explained more easily if one assumes, as does ALDEN (1942), an uterotubal sphincter, regulated hormonally.

During the passage of the fertilized eggs through the tuba, only slight differences in the development of the embryos can be proved in the females which were killed at the same interval after mating. The first time a greater variation in the degree of development of the blastulae could be proved, was among the three females which were killed 12 days after mating. This variation is shown by figs. 33—36, showing the blastulae from these three females. None of these females exhibited any progestational proliferation as an indication of impending implantation.

Autopsy was performed on three females 16 days after they had been mated, and all of them had blastulae which could be flushed out, but one of them had blastulae which showed a tendency to adhere to the uterine mucosa. In the last-mentioned case implantation had certainly already started, for with greater magnification primary chorionic villi could be detected in the form of a sparse down round the blastulae. For purposes of comparison, it may be mentioned that, according to STRAHL (1906), in ferrets the blastulae form chorionic villi already 10 days after mating. In mink at the implantation stage the blastulae show a typical tendency to shrivel immediately after being flushed out, and therefore it was not possible to obtain a picture of an intact blastula (compare fig. 38).—It is of interest that PINCUS (1936) states that the same thing is true of the blastulae in rabbits at the same time of implantation.—The variation in the blastulae of these females was very appreciable. Female No. 40, 1941, had blastulae with a diameter of 375 μ (fig. 37), and female No. 26,

VOL
28
194

1941, had blastulae with a diameter of 655 μ (fig. 38). Blastulae from the third female were intermediate.

Autopsy was performed on 4 females 20 days after they had been mated, one of them having been re-mated at an interval of 12 days. Females Nos. 32, 1941, and 24, 1941, had unimplanted blastulae whose degree of development corresponded with those shown in figs. 38 and 39. Female No. 35, 1941, had blastulae with the same tendency to adhere to the uterine mucosa as those in female No. 26, 1941, and exhibited the same degree of development. Thus in this female implantation had begun. Female No. 105, 1941, which was re-mated at a 12-day interval, had implanted foetuses among which was probably a monozygotic pair of twins (fig. 42). In view of the advanced development, it appears probable that implantation took place immediately after the blastulae reached the uterus, i.e. 8—10 days after the mating. Thus these females exhibit a variation in the point of time of implantation of at least 10 days.

Twenty-one days after they had been mated, autopsy was performed on two females Nos. 93, 1941, and 109, 1941, which had been re-mated at intervals of 8 and 11 days respectively. These females had implanted foetuses which had not reached quite such an advanced stage of development as those shown in fig. 41.

Autopsy was performed on three females 22 days after they had been mated. Of these females No. 12, 1942, had blastulae at the commencing implantation stage and a development corresponding to that shown in fig. 38. The other two females, Nos. 98, 1941, and 107, 1941, which were re-mated after an 8-day interval, had implanted foetuses whose degree of development appears from fig. 41.

Autopsy was performed on female No. 97, 1941, 24 days after she had been mated. She had implanted foetuses whose degree of development was not quite so advanced as that shown in fig. 42.

Autopsy was performed on four females 25 days after they had been mated. Of these, female No. 9, 1941, still had free blastulae in the lumen of the uterus. These blastulae corresponded very closely to those reproduced in fig. 38. Female No. 35, 1941, had swellings of the size of hemp seeds in the uterus, which showed that implantation had begun. Histological sections showed that chorionic villi had penetrated into the uterine glands (fig. 64). The two other females, which had been re-mated after 8 and 9 days respectively, had implanted foetuses. The foetal development in female No. 104, 1941, had advanced somewhat further than that shown in fig. 42, and in female No. 95, 1941, it corresponded to that shown in fig. 43.

Autopsy was performed on female No. 103, 1941, 29 days after she had been mated. She had implanted foeti, the development of which had not advanced quite so far as that shown in fig. 41.

Thirty days after they had been mated, autopsy was performed on four females, all of which exhibited implanted foetuses. Females Nos. 8, 1941, and 33, 1941, had foetuses whose development corresponded to that shown in fig. 40. On the whole the foetal development in females Nos. 38, 1941, and 43, 1941, had advanced equally far (fig. 43). Among the foetuses from No. 38, 1941, there was probably also a monozygotic pair of twins.

Autopsy was performed on one female 35 days after she had been mated. She had implanted foetuses (fig. 45).

Forty days after they had been mated, autopsy was performed on two females (figs. 44, 46). As appears from fig. 46, the foetuses from No. 16, 1941, were in a very advanced stage of development, and in this case parturition would have taken place in only a couple of days (cf. fig. 47).

Thus it was found that in several cases the variation in the rate of embryonic development in females which were killed at equal intervals after mating was so great that it cannot be explained otherwise than on the assumption that development had ceased entirely or been greatly reduced at some period or other. This becomes still more obvious if a comparison is made between the relative developments in the females killed at different intervals after mating. The two females Nos. 8 and 33, 1941, killed 30 days after mating, showed the embryonic development reproduced in fig. 40, while female No. 105, 1941, which was killed 20 days after mating, exhibited the embryonic development shown in fig. 42. Thus the last-mentioned female had considerably further developed foetuses than the two first-mentioned females, which were killed at a 10-day longer interval after mating. Several similar examples could be adduced. Thus, 25 days after mating, female No. 9, 1941, still had blastulae lying free in the uterus lumen, while in female No. 26, 1941, implantation had begun as early as 16 days after the mating. The last-mentioned case shows that the variation is due to variations in the interval between mating and implantation. This delay in implantation, in its turn, causes the great variation in the length of the gestation period.

The delayed implantation in the case of mink here described diverges from the corresponding phenomena in roedeer, badger, marten, ermine, the nine-banded armadillo, and other animals (see the following section), in that the free vesicle stage is shorter and of greatly varying duration. In that respect it recalls rather the delayed implantation met with in mice and rats, which is caused by the suckling of the young. The causes of the delayed implantation in mink will be discussed in a later section.

If the embryonic development in the once-mated females is compared with that in the re-mated ones, it is found that in the latter it shows a clear tendency towards acceleration. This implies that if a female is mated as soon as she exhibits estrus, the interval before implantation takes place is longer than if she is mated later. If this observation is correct, it should be found that females

VOL
28
194

which are re-mated at intervals of more than 7 days have a shorter gestation period than once-mated females. To investigate this matter, such females have been sorted out from the total Quebec material (described in section III) as were mated twice at intervals of at least 8 days. Thus these females ovulated again after the second mating (see p. 46).

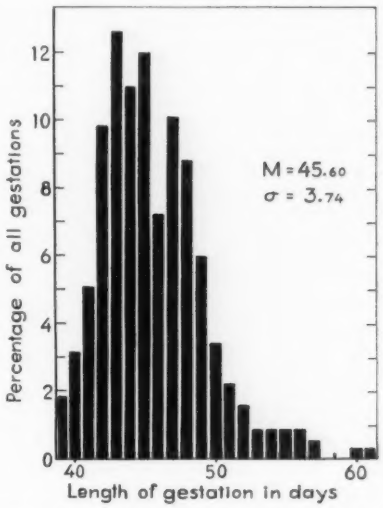


Fig. 48. Frequency distribution of the length of gestation in 324 re-mated Quebec females.

In fig. 48 the length and variation of gestation are shown for these 324 females. The average length is 45.60 days, as against 51.33 days for the once-mated (table 8, fig. 5). The gestation period shows a standard deviation of 3.74 days for the re-mated, as against 5.42 for the once-mated females. Thus for the re-mated females the gestation period is shorter and exhibits less variation than for the once-mated. However, these values are not quite comparable. As was shown in section III, the length of the gestation period decreases when the mating date is moved forward. It is in the nature of things that the re-mated females should be mated at a later point of time than the once-mated ones, and this contributes to the results arrived at above. To eliminate the influence of the mating date, the re-mated females have been arranged in table 20 according to the time of mating, and, for the purpose of comparison, the average figures for the once-mated Quebec females have been inserted. As appears from this table, the length of the gestation period is shorter throughout for the re-mated females. On an average the period is 2.6 days shorter. Thus, as the interval between the first and second matings averaged 11.8 days, the curtailment does not correspond to this interval. However, from the sexual point of view, the re-mated females may be different from the once-mated ones, and the dissimilarity may have affected the length of gestation. If this was the cause of the whole difference in the length of gestation, no correlation should be found between the length of the interval between the matings and the length of gestation. In table 21 the females have therefore been arranged according to the interval between the matings. This table shows that, with a longer interval between the first and the fertilizing mating, the period of gestation shows a clear tendency to become shorter. This shows that the length of the free vesicle stage also depends on the stage of estrus when the female is mated.

Table 20. *Influence of re-mating on length of gestation.*

	Date of fertile mating in March							
	10—11	12—13	14—15	16—17	18—19	20—21	22—23	24—25
Twice-mated females:								
Number of females . . .	9	17	53	56	59	37	55	38
Mean length of gestation .	48.3	47.2	47.9	46.8	45.9	44.1	43.3	42.7
Once-mated females:								
Number of females . . .	106	128	106	67	42	18	14	8
Mean length of gestation .	51.8	50.7	49 7	48.3	48.5	47.0	46.9	45.4
Difference	—3.5	—3.5	—1.8	—1.5	—2.6	—2.9	—3.6	—2.7

Table 21. *Influence of the length of the mating interval on length of gestation.*

	Length of the interval between first and second mating in days							
	8—9	10—11	12—13	14—15	16—17	18—19	20—21	22—
Number of females	68	114	73	39	11	8	9	2
Length of gestation	46.9	45.9	44.8	44.6	43.8	44.7	43.3	42.5

By way of summary, it may be said that the mink exhibits a delayed implantation, which leads to discontinuous embryonic development and a great variation in the length of the gestation period. The length of the free vesicle stage depends both on the time of mating, and on the interval between the beginning of the estrous period and the mating.

VII. DELAYED IMPLANTATION.

In mammals embryonic development is usually a continuous process. Ovulation is followed almost immediately by fertilization and the passage of the egg through the tuba. The cleavage of the fertilized egg begins already during the passage to the uterus, so that when it arrives there it has as a rule reached the blastula stage. As soon as the blastodermic vesicle has come into contact with the uterine mucosa, implantation and formation of the placenta begin. The cells of the blastocysts which are not concerned in implantation proceed with the formation of the embryo, which differentiates and grows continuously until the time of parturition. In sharp contrast to this continuous process is the discontinuous embryonic development in mink which was described in the preceding section, and which is also met with in some other animals. It is common to these that, after the fertilized egg has passed through the tuba, it

enters into a resting period, the length of which varies. In some cases this delayed implantation has no manifest cause, in others it only appears when the female is suckling a certain minimum number of young.

A. OCCURRENCE OF DELAYED IMPLANTATION.

As early as in 1854, BISCHOFF (1854) showed that the embryonic development in the roedeer was not continuous. This was verified by RETZIUS (1900) and KEIBEL (1902), who found that, after the mating in July—August, ovulation, fertilization and the passage of the eggs through the tuba took place in a normal manner. After ariving in the uterus, the blastula entered into a stage of relative rest, which lasted up to the middle of December, when the blastula was suddenly implanted, after which the embryonic development proceeded at a normal rate, until parturition in April. PRELL (1938) found that 22 roedeer which mated in July—August had gestation periods of 273—318 days, while 2 roedeer which mated in March—April had gestation periods of 150 days. Thus in roedeer the interval from ovulation to implantation is dependent on the time of mating.

A corresponding delay in implantation was found by FRIES (1880) and FISCHER (1931) for the European badger, Meles meles, and by HAMLETT (1932 a) for the American badger, Taxidea americana. The former mates in July—August, and the latter in August and September. In the case of the European badger implantation takes place at the end of January, after which parturition follows in March. In the case of the American badger implantation takes place in February and parturition in April. Thus, apart from the fact that the time of the sexual cycle is somewhat different for the two species, their reproduction corresponds exactly.

PATTERSON (1912, 1913) and HAMLETT (1932 b, 1935) found the same delay in implantation for the nine-banded armadillo, Tatusia novencincta. This armadillo, which is known especially for its polyembryony, mates in July. The free vesicle stage lasts up to the beginning of November, when implantation takes place. Embryonic development then continues at a normal rate until parturition at the beginning of March.

As appears from the introductory survey of the literature, a similar delay in implantation has also been shown for the stoat, Mustela erminea, by WATZKA (1940) and DEANESLY (1943), and for the long-tailed and short-tailed weasel, Mustela frenata et cicognani, by WRIGHT (1942 a, b).

In view of the mating conditions of the marten, PRELL (1927, 1931, 1938) assumed that there was delayed implantation, which has since been confirmed for the pine marten, Martes americana, by WRIGHT (1942 b), and for the western pine marten, Martes caurina caurina, by MARSHALL and ENDERS

(1942). According to MENKLEY (1942), these species of martens mate in July—August, and as both WRIGHT and MARSHALL and ENDERS found unimplanted blastulae up to January, the marten would seem to have a free vesicle stage of 5—6 months.

According to ENDERS, PEARSON and PEARSON (1946), there is also delayed implantation in the fur seal, and HAMLETT (1935) considers that there is also reason to assume that conditions are the same for the Siberian sable, Martes zibellina, the black bear, Euarctos americanus, the European brown bear, Ursus arctos, the grizzly bear, Ursus horribilis, and the polar bear, Thalarctos maritimus, but there is no experimental proof of this.

A serious objection can be raised against all the experimental investigations mentioned above. In all the cases the animals were killed in the wild state at different times of the year and their genitalia subsequently examined. There was therefore no checking of the time of mating. Even though this lack of knowledge of the antecedents of the experimental material cannot to any great extent have affected the interpretation of the results, it seems to be necessary to bear the facts in mind.

VOL
28
194

It is common to the cases of delayed implantation described above that it has no obvious explanation. On the other hand, the delayed implantation occurring in mice, rats, the common and the lesser shrew, and the bank vole, has a manifest explanation.

According to BRAMBELL (1937), as early as in 1882 LATASTE proved that, if a female mouse mated immediately after parturition and then suckled her young, gravidity was delayed. This phenomenon was subsequently studied more closely by DANIEL (1910), KIRKHAM (1915, 1916, 1918), ENZMANN, SAPHIR and PINCUS (1932), ENZMANN (1935), PINCUS (1936), BLOCK (1939) and DEANESLY and NEWTON (1941). From these investigations it appears that, when a female is mated again immediately after parturition, implantation is generally delayed if she suckles three or more young. On the other hand, there is no definite relation between the number of young suckled in excess of three and the total delay in implantation.

KING (1913) found similar conditions in rats, and his observation has since been confirmed by TEEL (1926), BRAMBELL (1937), KIRSCH (1938), KING (1938), WEICHERT (1939, 1940, 1942, 1943) and KREHBIEL (1941 a). In rats, however, implantation is not delayed unless the female is suckling 6 or more young, nor does there appear to be any definite relation between the number of young in excess of six and the total delay in implantation. KREHBIEL, who made a very careful study of these conditions, was able to prove by means of laparotomy that implantation in rats tends to be delayed by multiples of the length of the estrous cycle, implantation taking place at 6—8, 10—11, 14—16 or 18—20 days' intervals after mating.

BRAMBELL (1937) showed that delayed implantation, as a result of the female suckling her young subsequent to mating, probably occurs also in the common and the lesser shrew, Sorex araneus et minutus L., and the bank vole, Clethrionomys glareolus brittanicus M. However, there is no definite proof that this is the case, and PEARSON (1944) has shown that in all probability it is not the case with the American shrew, Blaurina brevicauda Say.

This survey shows that delayed implantation occurs in many different animals, but it is not, however, a consistent phenomenon. In mice, rats, the common and the lesser shrew, and the bank vole, it only occurs when the female is suckling a certain minimum number of young. In the roederer, the badger, the nine-banded armadillo, the stoat, the marten and the fur seal, the free vesicle stage is of considerable and, on the whole, constant length. On the other hand, in mink the length of the free vesicle stage varies very greatly, and in certain cases, as far as can be judged, implantation takes place at the normal time.

VOL.
28
1947

B. CAUSES OF DELAYED IMPLANTATION ACCORDING TO EARLIER INVESTIGATIONS.

Earlier it has been generally considered that, if a mated polyestrous animal again came in estrus, this was due either to the egg not having been fertilized or to its not being in a condition for implantation after fertilization. On the other hand, as a rule the possibility has been overlooked that the non-appearance of pregnancy may be due to a disturbance in the mechanism which regulates implantation. The occurrence of delayed implantation indicates that the implantation mechanism is less perfect than there has previously been a tendency to believe. In section V it is shown, too, that a fertilized egg, which is in the free vesicle stage, perishes if the female is caused to ovulate again as a result of mating. The circumstance that a polyestrous animal again comes in estrus after mating thus need not indicate that the eggs from the preceding mating were either not fertilized or were not in a condition for implantation, but may be due to the uterine mucosa not having been ready for implantation. Investigations by BALL (1940) proved that this is often the case with mice, in which copulation does not always elicit corpus luteum activity, with the result that the eggs cannot be implanted, although they are fertilized and have developed up to the implantation stage. Conditions appear to be the same in the case of e.g. the cow. In the case of both natural and artificial insemination, approximately two inseminations per pregnancy are required in cattle. It does not appear probable that this low rate of fertile inseminations is only due to a low fertilization percentage and deficient vitality of the fertilized egg. Among other things, the fact that cows often exhibit slight estrus even when implantation has taken place, indicates that the low rate of fertile matings may

be partly due to the uterine mucosa not having been sufficiently prepared for implantation.

As PINCUS (1936) pointed out, owing to the occurrence of a natural variation in the implantation time, possibilities have been opened for a direct study of the causes of implantation. It is true that earlier, by means of ovariectomies and hypophysiectomies combined with transplantations of glandular tissues and supplies of hormones, it has been possible to prove several endocrine interrelations in connection with implantation, but however skilfully these ectomies and transplantations may be carried out, they are still very clumsy interferences in the course of sex physiology. Therefore it is not probable that the finer details of the implantation mechanism can be analysed in this way alone. It appears probable that, in this respect, the delayed implantation may afford valuable supplementary aid. In spite of this, and in spite of the fact that the phenomenon of delayed implantation has long been known, it is actually not until recent years that it has been the subject of more exhaustive studies. Thus, in the latest edition of the eminent work "Sex and Internal Secretions", by ALLEN, DANFORTH and DOISY (1939), no mention is made of this phenomenon. Therefore a survey is given below of the results obtained from the earlier studies of delayed implantation.

The circumstance that, for the roedeer, the badger, and the marten, the breeding season occurs during the latter part of the summer and implantation after mid-winter, has given rise to different theories as to the causes of delayed implantation. For the roedeer and the badger, FRIES (1880) tried to explain this characteristic as an adaption for the benefit of the young. His argument was that it is necessary for the young to be born as early as possible in the spring, in order to become old enough to have a chance of surviving the following winter. As the winter is an unfavourable mating season, FRIES considered that the delayed implantation rendered mating under favourable conditions possible and resulted in the time of parturition being suitable. PRELL (1927, 1931) considers that the delayed implantation is a relic from the Ice Age. Owing to the shortness of the summer at that time, embryonic development had not time to take place. To prevent parturition occurring during the winter, which according to PRELL, would be fatal for the foetuses, embryonic development had to be retarded. Those species which exhibit delayed implantation have changed very little since the Ice Age, according to PRELL. MURR (1929, 1931, 1933 a, b) has severely criticised the hypotheses of FRIES and PRELL and considers that the delayed implantation is due to a change in the body temperature. In the case of the hibernating forms, such as the badger, it would be due to the general fall in body temperature, and in the case of the small marten or the thin-flanked roedeer it would be due to a deficient capacity for protecting the reproductive organs against cold. HAMLETT (1935) criticized these different hypotheses in detail and—basing himself on the conditions in the

nine-banded armadillo, whose delayed implantation was not known by FRIES, PRELL and MURR—was able to prove that none of them are tenable, possibly with the exception of that put forward by FRIES.

Bearing in mind the fact that implantation takes place at a time when the sun's radiation is on the increase, ENDERS and PEARSON (1943) and PEARSON and ENDERS (1944) tried to hasten implantation in marten and mink by means of irradiation.[1] In the experiments with the marten, Martes americana, 8 females were irradiated from 20th September in such a way that the duration of daylight + the irradiation time increased continuously. At the beginning of November the total light period was 16 hours. On 4th December laparotomy was performed on one female, which proved to have foetuses 11 mm in length. Two of the other females gave birth to 3 young each on 20th and 23rd December respectively. As the marten normally produces its young in April, the experiment undoubtedly showed that the irradiation had hastened implantation. The irradiation of mink took place before and after mating, and the results appear in table 22. There is a tendency towards a shortening of gestation, and this indicates that in mink, too, implantation was hastened by the irradiation.

Table 22. *Influence of illumination on length of gestation in mink, according to Pearson and Enders (1944).*

	Number of females	Mean length of gestation in days
Illuminated before and after mating	10	49.4 ± 0.29
„ only after mating	19	50.5 ± 0.49
Not illuminated, same herds in former years	20	54.7 ± 0.80
„ „ other herds	91	53.1 ± 0.37

The circumstance that in several animals implantation is delayed only if the female is suckling a certain minimum number of young led KIRKHAM (1915, 1916, 1918) to assume that the delay is due to the fact that up to the time of implantation the suckling young are obtaining all or most of their nutriment from the mother. Thus the suckling deprives the body of nourishment, so that implantation is rendered impossible. This conception is supported, firstly, by the fact that it is at the time of implantation that the suckling young require most nutriment, and secondly, by the fact that delayed implantation only occurs if the female is suckling a certain minimum number of young. On the other hand, as BRAMBELL (1937) pointed out, the requirements of nourishment for the foetuses during pregnancy are so slight that this can be

[1] Their experiment with mink was suggested by an indication in a preliminary note by the present author (HANSSON 1940) that the mink had delayed implantation. The irradiation experiment by PEARSON and ENDERS was actually carried out later than the present author's irradiation experiment with mink published in this work.

of no practical importance for lactation. If the time of implantation is studied for the badger, the roedeer, the marten and the ermine, it is found that in badgers it occurs during the hibernating stage, when metabolism is at its lowest, and in the others when the supply of food is at its shortest. Even though it is not certain that in these animals the delayed implantation is conditioned by the same factor as in the case of rats, mice, etc., these circumstances indicate that the relative supplies of nutriment are of no great importance for implantation.

Several workers have considered that the delayed implantation is due to a disturbance in the internal secretions, but opinions are very divergent on this point. Some consider that it is caused by too low an incretion of gonadotropic hormones from the anterior pituitary, others that the estrogen incretion is too low, and, finally, others that the corpora lutea do not increte sufficient progesterone.

In the matter of the delayed implantation occurring in association with lactation in mice, rats, etc., it is known from the classic work by LONG and EVANS (1922) that the female, when she is suckling her young, does not as a rule exhibit a fresh estrus. If she is mated and suckles a sufficiently large number of young, the corpora lutea do not develop fully until implantation takes place, and this also applies to mice (DEANESLY and PARKES 1931). A corresponding under-development of the corpora lutea during the free vesicle stage has also been found for the nine-banded armadillo by HAMLETT (1932 b, 1935), for the bank vole by BRAMBELL (1937), and for the stoat by WATZKA (1940) and DEANESLY (1943). HAMLETT says: "Despite its large size the corpus seems to be inactive, and this conclusion is supported both by histological study and by the completely negative result attending its removal during this period". On the basis of this under-development of the corpora lutea, various workers have tried to hasten implantation by means of the injection of progesterone. HAMLETT (1935) obtained a completely negative result from the injection of synthetic progesterone into mated armadilloes, and PINCUS (1936) and SELYE (1939) also obtained negative results from the injection of estrogen-free and synthetic progesterone into mice. WEICHERT (1939, 1940) injected 0.1—3.0 mg of synthetic progesterone daily into rats for 20 days after mating, and the result was a tendency towards a shortening of gestation, but, judging from the data of his experiments, it appears that the result was uncertain. Thus the relation of the corpora lutea to the delayed implantation has not been fully elucidated. A circumstance which has given rise to the opinion that, nevertheless, the corpora lutea are active during the free vesicle stage is that traumatization of the uterine mucosa in rats during this stage leads to the development of deciduomata (LONG and EVANS 1922). After GOLDSTEIN and TATELBAUM (1929) and others had shown that the precondition for the formation of such deciduomata is that the uterine mucosa is

under the influence of the corpus luteum hormone, BRAMBELL (1937) declared that "the theory that delayed implantation is due to inactivation of the uterus is clearly invalidated". However, TEEL (1926), LYON and ALLEN (1938) and KREHBIEL (1941 b), have pointed out that there may be a difference between the sensitization required for implantation and for the formation of deciduomata. As a support for that assumption KREHBIEL showed, after a careful cytological study of decidual tissue in the sterile horns of unilateral pregnant rats, that, during the free vesicle stage, more intensive irritation is necessary to provoke deciduomata than at the time when implantation takes place. Further, SYDNOR (1945) found that, if prolactin was injected into rats during estrus, traumatization of the uterine mucosa during diestrus led to the formation of deciduomata. This suggests the possibility that it is the incretion of prolactin from the hypophysis which renders the uterine mucosa sensitive to traumatization during the free vesicle stage. Thus this sensitivity to traumatization does not imply that the uterine mucosa is ready for implantation.

The non-appearance of estrus in rats and mice during the period when the female is suckling her young, indicates a suppressed incretion of estrogen. Guided by this and by the circumstance that in rats implantation appears to take place at intervals corresponding to the length of the estrous cycle, KREHBIEL (1941 a) drew the conclusion that estrogen was the determining factor in delayed implantation. This assumption derives a certain amount of support from the fact that the roedeer, marten and stoat exhibit estrus in association with the implantation itself. WEICHERT (1942), however, considered that the non-appearance of estrus during lactation is not due to too low an incretion of estrogen but to the estrogen being exhausted in connection with the secretion of the milk. LYON and ALLEN (1943) attempted to analyse the importance of the estrogen in the following manner. The uterine mucosa of female rats which were suckling young was traumatized 4—5 days after parturition, and as a result deciduomata were formed. If the females thus treated were traumatized on the 10th day after parturition, the uterine mucosa did not react again. LYON and ALLEN then supplied estrogen 9—11 days after parturition and traumatized the uterus on the 10th day. In these cases fresh deciduomata were formed. From this, the conclusion was drawn that failure of implantation during lactation and failure to obtain secondary deciduomata in the rat are both due to a relative estrogen deficiency. WEICHERT (1942, 1943) tried to attack this problem direct by supplying mated female rats, which were each suckling 9 young, with small amounts of estrogen and investigating how this affected implantation and the length of gestation. In one experiment with 123 females the estrogen was injected, but in another experiment with 10 females WEICHERT scattered small amounts of diethylstilbestrol about the cages. As a result of the treatment, the fertility was very low in both experiments. Thus, in the first experiment, of 57 females only 4

produced normal litters, and in the second, of 10 females only two produced normal litters. WEICHERT considered that in the first experiment the treatment led to normal implantation in 68 % of the cases, and a similar result also followed on the second experiment. According to WEICHERT, this shows that the delayed implantation in rats is due to too low an estrogen content in the tissue. The abnormal breeding results and certain other circumstances render it necessary, however, to judge WEICHERT's results with some caution.

BRAMBELL (1937) advanced the hypothesis that the delayed implantation is dependent on the blastula itself. According to him, the development of the blastula can be conceived as being dependent on some growth-stimulating substance like that known to occur in certain embryonic tissue extracts. In support of this hypothesis, BRAMBELL adduces that in the shrew the growth of the blastula ceases before it has reached the implantation stage. On the other hand, KEIBEL (1902) and FISCHER (1931) considered that they had found that the development of the blastula in the roedeer and badger never ceases entirely during the free vesicle stage, and similar conditions appear to prevail also in the case of mink. Retardation of embryonic development during the free vesicle stage may be due equally well to a check in the supply of nourishment as to an absence of growth-stimulating substances.

WEICHERT (1939, 1940) found that gonadotropic substance prepared from pregnancy urine (PU), alone and in combination with progesterone, and injected 8—20 days after mating into lactating rats, led to a tendency towards curtailment of pregnancy. HAIN (1932) and KING (1938) arrived at directly contrary results from the injection of the same substance into lactating rats. They found prolonged gestation owing to delayed parturition, and as a result of this a great foetal mortality. SNYDER (1934) and HOOPER and KING (1935) arrived at exactly the same result after the injection of the same substance into female rabbits, and TEEL (1926) and HAIN (1932, 1934) after the injection of extract from the anterior pituitary into lactating rats.

As appears from this survey, opinions are divided as to the causes of the delayed implantation. The experimental investigations have not yielded uniform results. This applies to the effect of progesterone, estrogen, and other substances, on the delayed implantation. There is much which speaks in favour of the primary cause of the delayed implantation being a change in the incretion in the anterior pituitary. In earlier investigations such a possibility has only been touched upon in passing by WEICHERT (1939, 1940).

As the earlier investigations did not yield uniform results, and as it cannot be taken for granted that the delayed implantation in the case of mink is caused by the same internal factors as the delayed implantation in mice and rats, these earlier investigations have only been a slight guidance for the present writer's investigations. However, the former have shown the complicated nature of the problem, and therefore the present work has been concentrated on

VOL
28
194

attacking the problem from different angles. This has been done, firstly, by statistically and experimentally investigating the influence of outside temperature and of light on the delayed implantation, secondly, by studying the changes in the histological picture of the ovaries, tuba, uterus and vagina, during the sexual cycle, and thirdly, by studying how different hormones and gonadotropic substances affect mated, normal and ovariectomized females.

C. EXTERNAL FACTORS IN DELAYED IMPLANTATION IN MINK.

The external factors which, in the first place, may conceivably affect implantation are nutrition, temperature and light conditions. In the case of mink the food certainly varies very greatly from year to year and from farm to farm, but as a rule on one and the same farm all the animals receive similar food, and this is not systematically changed during the mating season. The length of gestation varies very greatly, however, for females which are mated on the same day, and which consequently receive similar food. Further, as appeared in section III, there is a seasonal trend in the length of gestation, and this cannot be attributed to any change in the food. As this is very strong evidence that the food does not cause any appreciable variation in the length of gestation, this factor has not been studied. On the other hand, in earlier investigations temperature, and very especially light, proved to affect the sexual functions, and therefore the influence of these factors, on implantation were studied more closely.

1. TEMPERATURE.

In an experiment with ferrets, MURR (1931) found that a rise in the outdoor temperature led to a tendency towards a shortening of gestation. Only 6 females were comprised in the experiment, however, four of them becoming pregnant. A rise in the outdoor temperature of 15° led to a shortening of the gestation period by 2 days. In view of the inconsiderable number of experimental animals, this result may very well be a matter of chance. There are no other investigations showing the influence of temperature on the length of gestation.

As was mentioned in section III, breeding data for 697 females, described as "once mated", was obtained during the years 1939—1941 from A. B. Mink, Lidö Säteri. During these years the outdoor temperature varied greatly before and during the mating seasons. As a check in this variation in temperature, particulars were obtained from a meteorological station situated in the neighbourhood of Lidö Mink Farm. The length of gestation for these 697 females has been correlated in various ways with the information as to temperature,

in an endeavour to elucidate whether the outdoor temperature has any influence on the length of gestation.

A statistical analysis showed the following correlations between the length of gestation and the mean temperature during the intervals given below, reckoned from the day of mating:

Mean temperature during the period 20 days before the day of mating, $r = -0.080^{*}$
" " " " " 10 " after " " " " $r = -0.019$
" " " " " 20 " " " " " " $r = -0.092^{*}$
" " " " " 40 " " " " " " $r = -0.236^{**}$

As is seen, with a rising temperature there is a decreasing gestation period. The uniform course in the correlation series also indicates that there is such a relation. Unfortunately, however, this correlation may have been caused by a co-variation of the temperature and the rays of the sun.

To attempt to eliminate the effect of the rays of the sun, an analysis of variance was made within dates of mating (table 23) (cf. table 12). It is

Table 23. *Analysis of variance of length of gestation.*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Ratio of mean squares
Between dates of mating . . .	32	7980.8	249.40	
Within " " "				
Between years	44	1405.0	31.93	$\frac{31.93}{17.51} = 1.82^{***}$
Within " (error)	620	10855.3	17.51	
Total	696	20241.1	29.08	

Table 24. *Influence of date of mating on length of gestation in different years.*

Date of mating	1939		1940		1941	
	Number of females	Mean length of gestation	Number of females	Mean length of gestation	Number of females	Mean length of gestation
Mch. — 4	19	59.7	13	59.9	6	63.2
5— 8	39	52.9	21	57.0	58	55.0
9—12	80	50.5	57	53.2	73	52.7
13—16	26	48.9	52	50.2	129	49.1
17—20	12	46.2	44	49.3	26	47.2
21—24	8	45.4	16	46.8	3	48.0
25—28	4	50.5	7	45.4	2	44.0
29—	1	46.0	1	48.0	—	—

based on the circumstance that during the three years 1939, 1940 and 1941 the temperature varied very considerably. Thus during March 1939 the average temperature was —0.80° C, in 1940 it was —5,73° C and in 1941 it was —4.80° C. These differences in temperature were probably not caused by a variation in solar radiation, but by currents of cold air. Therefore, if a cause of variation can be proved within the mating dates between years, it will have been caused by the temperature. As appears from table 23, there actually is such a significant cause. Therefore the length of the gestation period for the same mating date should be shorter during the warm year 1939 than during 1940 and 1941. In table 24 and fig. 49 the material has been distributed over the three years and the results are in accordance with the hypothesis of a temperature influence. If the mean difference in length of gestation in relation to the date of mating are calculated for the three years it emerges that during the warm year 1939, for the same mating date, the length of gestation was 2.32 days shorter than during the coldest year, 1940, and 1.78 days shorter than during the year 1941.

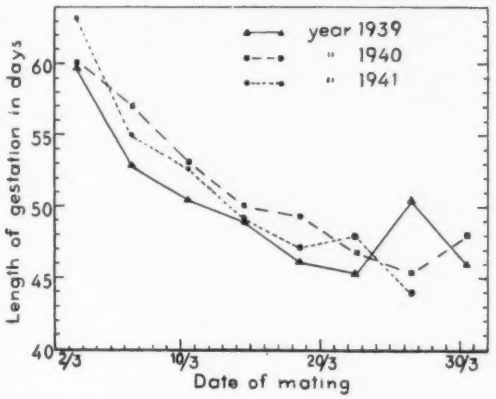


Fig. 49. Relation between date of mating and length of gestation in different years.

VOL. 28 1947

2. LIGHT.

A very great number of investigations into the influence of light on the sexual functions of different animals have been carried out. A general survey of the literature in this field has been given by MARSHALL (1942). In this connection, therefore, only the investigations will be touched upon which are of direct interest for the present writer's experiments.

BISSONNETTE (1932, 1935) showed that, if female ferrets were subjected to ordinary electric light for 6—6 ½ hours every evening during anestrus, estrus began after 38—64 days, and the females permitted mating, ovulated, and became pseudo-pregnant. He also showed that, if the length or intensity of the lighting was decreased after the females had started estrus, a regression took place towards the anestrus stage, but that, if the lighting was increased again, the females again came into estrus. MURR (1935) has criticized BISSONNETTE's experimental methods, and he is of the opinion that the effect observed in these experiments might have been due to the illumination having

raised the outdoor temperature, and that this rise in temperature might have led to the results obtained.

MARSHALL and BOWDEN (1934) irradiated female ferrets during anestrus with lights of varying wave-lengths and found that lights with longer wave-lengths than 6,500 Å had no effect. The shorter the wave-length, the greater the activation of the sexual functions. A blind female did not react to irradiation, which was considered to indicate that the eye was the organ through which the effects of irradiation made themselves felt. If, before estrus, females were placed in semi-darkness, estrus did not appear. In a later work MARSHALL and BOWDEN (1935) found that ultra-violet irradiation during pro-estrus hastened the onset of estrus and prolonged it. Certain results also indicated that it was not the length of the irradiation alone which was decisive for the activation capacity, but the product of the intensity and the length of the irradiation. This observation was also made by MARSHALL (1940).

The previously mentioned investigations by ENDERS and PEARSON (1943), and by PEARSON and ENDERS (1944), showed that light affected implantation in the marten and the mink. STEVENSON (1946) denies the effect of sunlight on sexual phenomena, basing himself on a field experiment with mink. Because the original paper is not available, it is impossible to judge the value of this finding.

LE GROS CLARK, MCKNOWN and ZUCKERMAN (1939) carried out resection on the optic nerves of ferrets during anestrus. After the operations the females were irradiated with ordinary electric light for 6 ½ hours every day. At the same time a number of control females, which had not been operated on, were irradiated during anestrus. After the irradiation all the control females exhibited estrus. Four females whose optic nerves were severed immediately behind the eyeballs all exhibited extremely slight symptoms of estrus after irradiation. One of these females mated, but the mating did not lead to ovulation. The females whose optic nerves were severed in different places in the brain all exhibited normal estrus after a somewhat prolonged irradiation period. From this the conclusion was drawn that the impulses towards activated sexual functions which the light elicits in the eye, may pass by way of other nerve paths in the brain than those serving the sense of sight.

It appears from the investigations referred to that light undoubtedly has a marked influence on the sexual phenomena, perhaps in the first place in such a way that the changes in the length and intensity of daylight regulate the time of the sexual cycle. To investigate whether the same conditions prevail also in mink, in 1941—1942 experiments were made with the irradiation of mink during anestrus and before and after mating.

a. Irradiation during anestrus.

During late anestrus, i.e. from 4th December, 1941, to 15th January, 1942, an experiment was made with ultra-violet irradiation of both males and females.

The experiment comprised, firstly, 5 groups of 4 older females each, which were irradiated for different periods (see table 25), secondly, 6 males, which were irradiated for 80 mins. every day, and thirdly, 20 older control females, which were not irradiated at all. For the irradiation was used an ultra-violet lamp of the type "original Hanau, reflector model SR 300" with an energy consumption of 575 watt. In order to avoid any affect of temperature, the irradiation was carried out in a large roofed-in space. During irradiation the animals were placed in wire-netting cages, whereby the possibilities of the animals avoiding the irradiation were eliminated. The lamp was placed 1 ½ metres above the floor, so that the reflector threw the light over a circular surface on it, the cages being placed within this irradiated area. The irradiation was given twice daily: immediately before sunrise and immediately after sunset.

MARSHALL and BOWDEN (1934, 1935) and MARSHALL (1940) took the swelling of the vulva of ferrets as the criterion of the effect of irradiation. In mink this change is very inappreciable. Therefore, instead, the changes in the composition of the vaginal smear were chosen for the control of the state of estrus.

Table 25. *Influence of irradiation during anestrus on size of ovary and cornua uteri.*

Length of irradiation in minutes per day in the groups	Number of females	Number of autopsied females	Mean of length × width in mm of	
			Ovary	Cornua uteri
No irradiation	20	10	8.72	1.74
40 minutes irradiation . . .	4	4	14.13	3.34
60 „ „ . . .	4	2	14.91	1.57
80 „ „ . . .	4	2	15.01	3.79
100 „ „ . . .	4	3	14.44	3.08
120 „ „ . . .	4	4	15.47	4.03

The experimental animals appreciated the irradiation, for they rolled about in the light and cooed, which they do not do otherwise at this time of the year. In the case both of the irradiated females and of the non-irradiated ones, the investigations of the vaginal smear showed that they changed from the typical anestrus appearance at the beginning of the experiment to different stages of advanced proestrus at the end. Even the females that had been exposed to the least irradiation exhibited a tendency towards a more rapid change to the proestrus stage than the non-irradiated females. This tendency was still more strongly marked in the case of those irradiated for the longest period. At the end of the experiments, the females which had been irradiated for 80 minutes and longer daily exhibited a vaginal smear which could not with regard to

the cell content be distinguished from that of the vaginal smear during estrus. At that time those which had been irradiated for a shorter time and the non-irradiated exhibited a smaller number of cornified cells, and the cornification was less pronounced (cf. page 97).

During the course of the experiment, regularly repeated attempts were made to mate both the non-irradiated and the irradiated females, the irradiated males being used. The non-irradiated females exhibited no willingness to mate. On the other hand, some of the irradiated females appeared to be willing. However, no mating took place, for when a female proved willing, the male proved unwilling, and vice versa.

When the experiment was discontinued on 15th January, autopsies were performed on 10 control females and 15 irradiated females, (table 25). From each female one ovary and a central segment of an uterine horn were fixed and sectioned. The vascularization of the sexual organs of all the irradiated females was more abundant than that of the non-irradiated. The histological pictures of the ovaries showed that the irradiation had led to an increased vascularization and a dilatation of the vessels. The follicular growth had been activated, but only a few follicles had reached the vesicular stage. The transverse sections of the uterus exhibited a thickened muscularis and mucosa, but the changes had not fully reached the estrus stage. This explains why no mating took place.

As the histological pictures in both the control females and the irradiated females exhibited a fairly considerable variation, measurements of ovaries and uterine horns were made, in order to investigate whether the changes in the size of the organs resulting on the irradiation were significant. For each female the long and the short axes were measured, firstly, in the largest section of the ovary, and secondly, in a cross-section through the cornua uteri. In order to express the size of the organs in one figure, the product of the lengths of the two axes was computed. These values are collocated in table 25 and the ana-

Table 26. *Analysis of variance of size of ovary and cornua uteri (from table 25). The material in the two groups, irradiated and non-irradiated females.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Ratios of mean squares
Ovary: Irradiated v. non-irradiated females	1	10442.53	10442.53	$\frac{10442.53}{460.99} = 22.65^{***}$
Within groups	23	10602.82	460.99	
Total	24	21045.35	876.89	
Cornua uteri: Irradiated v. non-irradiated females	1	4687.78	4687.78	$\frac{4687.78}{252.00} = 18.60^{***}$
Within groups	23	5795.99	252.00	
Total	24	10483.77	436.82	

lysis of variance is shown in table 26. These show that the irradiation had led to a considerable change in the size of the ovaries and the uterine horns. On the other hand, no definite relation between the length of the irradiation and the size of the organs could be proved. A remarkable circumstance is that the cornua uteri of the two females which had been irradiated for 60 minutes were completely unaffected.

Thus, by way of summary, it may be said that ultra-violet irradiation of mink during the late anestrus influences the sexual functions in the same direction as BISSONNETTE (1932, 1935), MARSHALL and BOWDEN (1934, 1935), LE GROS CLARK, MCKNOWN and ZUCKERMANN (1939) and MARSHALL (1940), found for ferrets.

b. Irradiation before and after mating.

Similarly, during the period from 15th February to 10th March, 1941, an experiment was carried out with ultra-violet irradiation. Two groups, each consisting of 10 older females, were used in the experiment. All the females at Lidö Mink Farm could be utilized as the control material, the experiment being carried out there.

In this experiment the irradiation was given with two ultra-violet ray lamps of the same design as in the previous experiment. In this case, too, the irradiation took place in an open animal shed to avoid the effect of temperature. The experimental animals were placed in wire-netting cages, and the lamps were placed on opposite sides of the cages at a distance of 4.0 metres from each other. As in the previous experiment, the females were irradiated before sunrise and after sunset. The total irradiation time per day was 45 mins. for one group and 90 mins. for the other. After some days' irradiation, some of the females that were receiving the long irradiation exhibited signs of blindness, and therefore the period of irradiation was curtailed somewhat. One of these females was removed from the experiment entirely. After a couple of days all signs of blindness had disappeared.

The irradiated females mated early in the season, which may possibly be ascribed to the irradiation. All the females mated and 15 of them had litters.

When studying the effect of irradiation on the length of gestation, consideration must be paid to the time of mating, in view of the relation which exists between these variables. This was done in such a way that the gestation period of each female was compared with the gestation period of the non-irradiated females which were mated on the same day. This gestation period has been called the "expected gestation period". However, 4 of the females mated as early as on the 23rd of February, and the non-irradiated females which were mated on the same day were all re-mated. In consequence there is no comparison material for this mating date. These 4 females have therefore been excluded from the comparison. In table 27 are shown the actual

Table 27. *Influence of irradiation before and after mating on length of gestation.*

	Length of irradiation in minutes per day	
	45	90
Number of females	7	4
Actual mean length of gestation	53.86	44.25
Expected „ „ „ „	55.89	54.27
Difference in days	2.03 ± 1.59	10.02 ± 1.01

and the expected gestation periods for the two groups of females, as well as the difference and its mean error. As appears from these values, the irradiation led to a marked curtailment of gestation. If the difference is compared with its mean error, there is a statistically significant difference for the animals which received the longest periods of irradiation.

In view of the similar results obtained by PEARSON and ENDERS (1944) in their irradiation treatment of marten and mink, it appears to be established that the irradiation of mink during pro-estrus and estrus promotes implantation. This is further confirmed by the positive results of the irradiation of mink during anestrus.

D. HISTOLOGICAL CHANGES IN THE FEMALE SEX ORGANS CORRELATED TO THE DELAYED IMPLANTATION.

The various phases of reproduction are reflected in cyclic changes, both in the ovaries and in the tuba, uterus and vagina, and therefore by studying these changes, valuable information can be obtained as to any possible divergence in reproduction and its causes. In this connection, especially the divergencies relating to the delayed implantation are of importance.

1. OVARY.

In foregoing sections the general anatomy and histology of the ovary and the development of follicles have been discussed. Here the development of the corpora lutea and the changes of the size of the ovary in relation to the sexual cycle will be described.

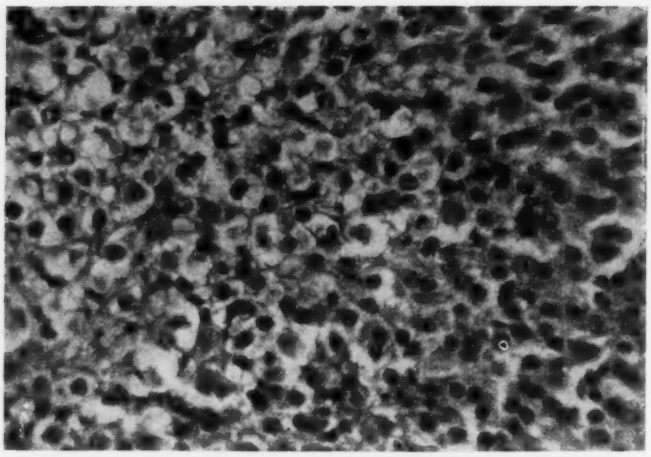
a. Development of the corpora lutea.

The conflicting ideas about the histogenesis of the corpora lutea and the greatly divergent conceptions as to which cell elements, the theca interna or granulosa cells, are the site of the formation of the corpus luteum hormone, were finally settled by a brilliant investigation by WESTMAN (1929 a). He

showed that, if the whole granulosa layer was removed from a follicle, no corpus luteum was formed, and there was no pregnancy reaction in the uterus. If, when the granulosa layer was removed, some remnant of it remained, a partial corpus luteum was formed, and a corresponding reaction in the uterine mucosa could be observed. Consequently the granulosa layer forms the luteal tissue, which in its turn is the site of progesterone incretion.

As a rule it has been assumed that ovulation elicits proliferation in the granulosa layer, and with it the formation of the corpus luteum. However, WALTON and HAMMOND (1928) showed that in rabbits, if a fully developed follicle was opened without mating having taken place, no corpus luteum was formed, but that if the female was mated before the follicle was opened, a corpus luteum developed. This proves that the formation of the corpus luteum cannot be considered an isolated phenomenon which is elicited by the rupture of a follicle, but that, in rabbits at any rate, it is conditioned by factors, probably of an endocrinous nature, which assert themselves already before ovulation. Therefore the renewed proliferation activity in the granulosa layer during the pre-ovulation stage found in the follicle development in mink is probably the prelude to the formation of the corpus luteum.

Immediately after ovulation, the granulosa layer spreads out towards the centre of the antrum folliculi. The whole of this tissue is loose and consists of cells connected with each other by cytoplasm structures, which are mainly arranged radially. This tissue becomes increasingly sparse towards the interior of the follicle, and for some time after ovulation there remains in the follicle a vacuole filled with fluid, which extends from the centre towards the rupture. The viscosity of this fluid is greater than that present before ovulation and appears to correspond exactly to the tertiary liquor folliculi which ROBINSON (1918) proved in ferrets. In connection with ovulation, complete changes also take place in the theca layer. The basement membrane which delimits the theca layer from the granulosa layer is penetrated by invading blood capillaries and theca cells of the nature of connective tissue. This membrane is completely disintegrated at a very early stage. The inner theca layer, which, in the follicle ready for ovulation, consisted of an outer zone of loose connective tissue, interspersed with polygonal cells and lymph sinuses, and an inner zone of an almost continuous vascular layer, also shows a tendency to disintegrate in connection with ovulation. Already 12—18 hours after ovulation, this layer has practically disappeared by migration into the granulosa tissue, and only the theca externa remains as a delimited sheath round the follicle. The whole follicle vacuole has gradually filled up with granulosa tissue and exhibits a fairly homogeneous structure. Up to the time when incretion activity has reached its maximum, however, a denser granulosa tissue can still be proved in the periphery of the corpus luteum than in its centre.



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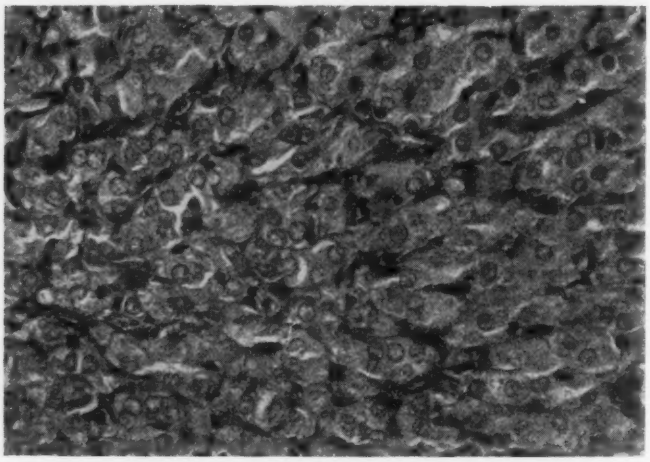

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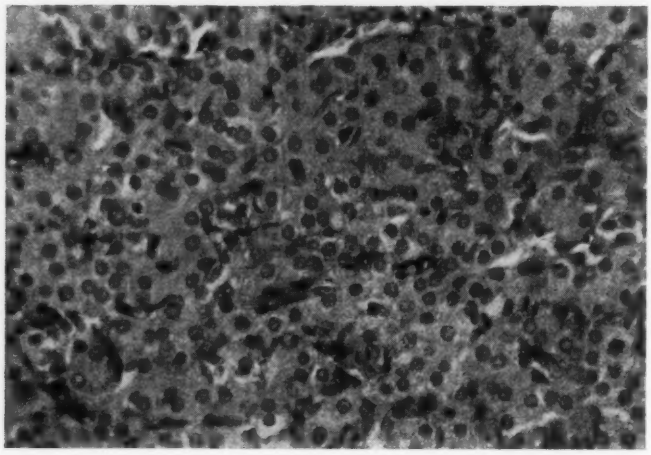
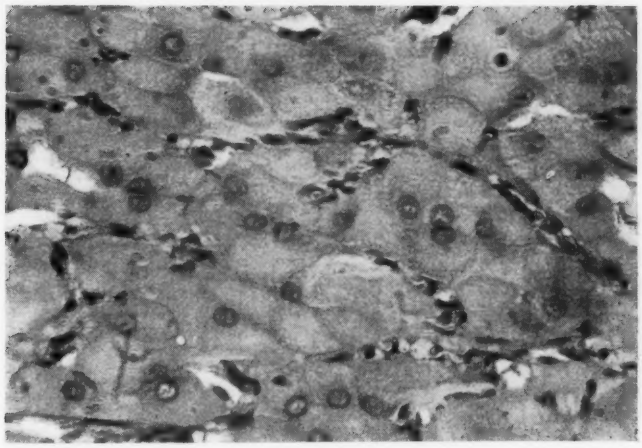


52

VOL
28
194



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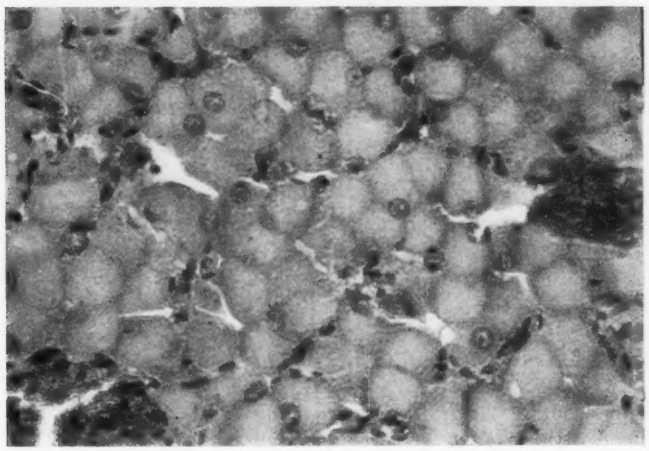


54

VOL.
28
1947

Figs. 50—54. Sections through the corpus luteum: — 50. During the proliferation phase of the granulosa. — 51. During the proliferation phase of the vascular system. — 52. During the inactive phase. — 53. During the incipient-increation phase. — 54. During the increation phase. (Hemalun-eosin stained, greenfilter, 360 ×.)

The study of the differentiation of the corpus luteum comprises, firstly, a scrutiny of the progress of vascularization, and secondly, the change in the granulosa or luteal cells. The histological picture of the corpora lutea of a female varies somewhat from body to body and within a body from periphery to centre. This study was therefore carried out as follows: firstly, all the sections of a female's corpora lutea were scrutinized, and then a representative one was selected and photographed with 180 times magnification. Similar photographs were taken for all the females which were of interest. A scrutiny of this material showed that, from ovulation until the corpus luteum was fully developed, five or possibly six different stages could be distinguished, which were characterized by the following properties.

1) *The proliferation phase of the granulosa.* As appears from the designation, this is characterized by proliferation of the granulosa, which proceeds until the antrum folliculi is filled with tissue. This proliferation takes place with such immense rapidity that, as a rule, even a few hours after ovulation, nearly the whole of the follicle vacuole is filled with tissue. A section from this stage is shown in fig. 50. The female in question was killed 3 hours after ovulation. The cell contours were still diffuse. The whole tissue may be characterized as a confused aggregation of cells without any ordered supply of blood vessels.

2) *The proliferation phase of the vascular system.* The granular proliferation is continuously followed by an ingrowth of vessels with accompanying strands of spindle-shaped cells. This phase continues up to 6—7 days after copulation. In fig. 51 is shown a section from this stage, taken 6 days after mating, i.e. when the plexus of vessels is almost built up. As appears from this section, the vessels have split up the tissue into irregular nests. The nuclei of the lutein cells are less basophilic than in the preceding stage and the cell territories obviously larger per nuclear unit.

3) *Inactive phase.* In contrast to what is the case in other animals, with the exception of the stoat (WATZKA 1940, and DEANESLY 1943) and possibly the nine-banded armadillo (HAMLETT 1935), the corpora lutea in mink, after the proliferation phase of the vascular system, pass over into an inactive stage, during which even a certain involution can be observed (fig. 52). In this stage the lutein cells are small, with dense and strongly basophilic cell nuclei. That the corpora lutea are inactive during this phase is confirmed by the fact that no progestational effect can be found in the endometrium and that the female allows mating and ovulates, by the estrous picture of the vaginal secretion, and by the absence of implantation. This stage persists until immediately before implantation.

4) *Incipient-increction phase.* At a stage when the blastodermic vesicles are still lying freely in the uterus, but when the uterine mucosa shows progestational modifications, the corpora lutea exhibit increasing activity (fig. 53). The lutein cells increase in volume. The nucleus is larger and less basophilic, the blood

VOL
28
194

capillaries are dilatated, and the whole tissue gives the impression of commencing activity.

5) *The incretion phase.* The further development, which coincides with implantation but continues even after it, is characterized by a very great infiltration of blood vessels. The volume of the lutein cells increases greatly, and they become pear-shaped in appearance, with the cell nuclei situated excentrically (fig. 54). The whole tissue gives an impression of great activity.

The corpora lutea remain in this stage up to some days before partus, when an incipient regression is perceptible, first showing itself in a decrease in the volume of the lutein cells and an increased number of strands of connective tissue penetrating into the corpora lutea. The involution of the corpora lutea after partus has not been studied.

b. Size of the ovary during the sexual cycle.

The cyclic changes in the evolution and involution of the follicles and the corpora lutea are reflected in the total volume of the ovaries. Measurements have been made of sectioned ovaries for the purpose of arriving at a conception of the magnitude of the variation. The sections ran parallel to the median plane of the ovary, i.e. dorso-ventrally and cranio-caudally. With a few exceptions the section thickness was 7 μ, and 3—4 sections per mm were mounted. The largest section from each ovary was selected, and its length and breadth were measured in a twelve-fold enlargement. Altogether 461 ovaries from 286 females were measured, but as some of these females had been included in experiments with ultra-violet irradiation, or treated with hormone, or were ill when killed, the number of untreated completely healthy females whose sexual stage could be established with certainty, was reduced to 164, the number of sectioned and mounted ovaries being 304.

In table 28 these females have been grouped according to the sexual stage, and for each stage are given the number of females and ovaries and the mean lengths and mean widths in mm of the ovaries. The product of the width and length of the ovaries of each female has been computed, and the means of these products are given as percentages of the corresponding mean during anestrus.

During anestrus, when the ovary is at rest, no vesicular follicles are found as a rule. The follicles which have advanced beyond stage 1 (p. 35) during this period of rest, exhibit atresia in the great majority of cases. The zona pellucida shrinks, the cytoplasm of the ovum is filled with fat droplets, and the ovum often shows signs of an atypical progressive development. The connective tissue elements of the theca and blood capillaries penetrate the basement membrane and invade the degenerating epithelium. The blood supply during this period is scanty. As appears from table 28, in this stage the length and width of the ovary are minimal.

Only a few females were killed during pro-estrus, and as this stage represents a phase of progressive activization of the sexual functions, and as it cannot be determined with certainty what point in this stage a female has reached when she is killed, these females have not been included. The size of the ovaries during this period, however, must be intermediary between anestrus and estrus, owing to the proceeding growth of the follicles.

Nine females were killed during estrus. Their ovaries were larger than during anestrus, but the difference was surprisingly small. This is due to the fact that in mink, as in ferrets (ROBINSON 1918), the follicular development during the vesicular stage is so intimately dependent on mating. The average relative section surface in this stage is 111.2.

Table 28. *Size of ovary during different sexual stages.*

Sexual stage	Number of		Ovary		
	Females	Ovaries	Length in mm	Width in mm	Relative size
Females autopsied in anestrus	22	27	4.17	2.57	100.0
„ „ in estrus	9	18	4.31	2.77	111.2
„ „ after mating, but before ovulation	10	20	4.82	2.75	147.6
„ „ 0—12 hours after ovulation	6	12	4.43	2.71	111.8
„ „ 1/2—7 days „ „	17	33	4.74	3.02	133.4
„ „ during the free vesicle stage	56	109	4.51	2.84	119.0
„ „ during the placental stage	24	47	5.21	3.09	150.0
Unmated females autopsied at the end of the mating season	11	20	4.59	2.92	125.8
Autopsied pseudopregnant females	9	18	4.37	2.71	115.7

During the interval between copulation and ovulation, an enormous follicular growth takes place, and as a result the relative section surface of the ovaries increases to 147.6. In connection with ovulation the follicles collapse, and some hours after ovulation the proliferation in the granulosa section is so advanced that the collapsed antrum folliculi is practically filled out. During this interval the relative section surface of the ovary is 111.8, or practically the same as in the estrus stage. The proliferation in the granulosa and the vascularization of the corpus luteum continues during the time when the egg passes through the tuba. During this phase the relative section surface of the ovary is 133.4. As a rule, after the egg has reached the uterus, an inactive phase of the corpora lutea sets in, and as a result the relative section surface of the ovary decreases, though not down to the surface of the estrus stage, but on an average to 119.0. Females with implanted foetuses always have fully developed corpora lutea, and in consequence the relative section surface of the ovary reaches its maximum, i.e. 150.0, during this phase. If it is assumed that the ovary is

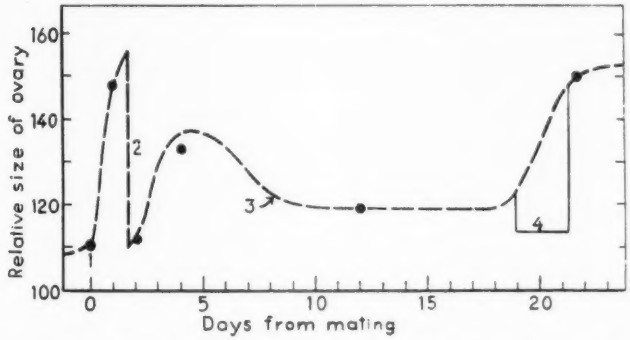


Fig. 55. Schematic illustration of the changes in the relative sizes of the ovary during the sexual cycle. The dots correspond to the values in table 28. *1* copulation, *2* ovulation, *3* the corpora lutea entering the inactive stage, *4* the corpora lutea entering an active incretion stage, which is followed by implantation.

changed equally in all directions, this implies that the volume is 1.85 times as large as during anestrus. In the case of ferrets ROBINSON (1918) gives an enlargement of 3.3 times, but he compared the anestrus volume with the greatest ovary volume in any female during gestation. As the ovary exhibits considerable individual variation, ROBINSON naturally obtained too high a value. In fig. 55 the variation in the surface of the ovary is shown schematically.

Further, in table 28 is given the size of the ovaries in females which were not mated during the mating season, and which were killed after it. As these ovaries contain cystic follicles, the relative section surface is greater than during estrus. Similarly the size of the ovaries in pseudopregnant females was determined. This group of females were, however, at different stages. In some the corpus luteum development had not yet reached its maximum, and in others the corpora lutea had already begun involution.

To analyse the statistical significance of the changes described here and to investigate whether the ovaries in one and the same female are more equal in size than the ovaries from different females at the same sexual stage, an analysis of variance was made on the basis of the product of the long and short axes of the section of the ovary; the results are shown in table 29. As

Table 29. *Analysis of variance of the size figures of the ovaries from table 28.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Ratios of mean squares
Between means of sexual stages . .	8	680.91	85.11	$\frac{85.11}{21.66} = 3.93^{***}$
Within „ „ „ „ . .	295	4031.69	13.67	
Between individual female means .	155	3357.66	21.66	$\frac{21.66}{4.81} = 4.50^{***}$
Within females	140	674.03	4.81	
Total	303	4712.60	15.55	

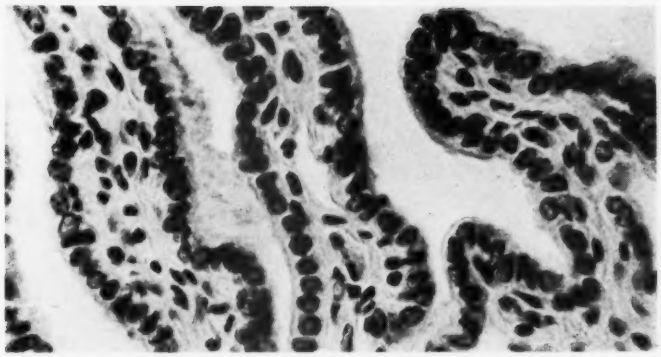
appears from this, there is a highly significant difference in the sizes of the ovaries between the various sexual stages. It is also found that within one and the same sexual stage the mean square is significatively greater between than within females. The intra-class correlation calculated on the basis of these mean squares is 0.648. This individual difference in the size of the ovaries is of course partly due to the fact that each sexual stage represents a phase of development which, without any definite borderline, passes over into the next. But apart from the correlation which arises from the impossibility of making the grouping sufficiently exact, there is undoubtedly an individual difference in the size of the ovaries.

2. TUBA UTERINA.

It has long been known that the mucosa of the tuba, and in the first place its epithelial layer, exhibits cyclic changes which are correlated with the sexual cycle, (MOREAUX 1913, LONG and EVANS 1922, ALLEN 1922, SNYDER 1923, 1924, AGDUHR 1927, COHEN 1927, WESTMAN 1929 b, 1930, 'ESPINASSE 1935, ALLEN, HISAW and GARDNER 1939 and Alden 1942). For the purpose of investigating whether similar changes can be proved in mink, a study was made of the histological material. As the epithelium in the tuba of the mink changes gradually from the infundibulum to the tubo-uterine junction, the comparisons between the different stages were made, firstly, on the basis of a transverse section through the ampulla, and secondly, on the basis of a transverse section through the central part of the isthmus. Measurements were made of the height of the epithelial cells and the diameter of the nucleus (cf. SNYDER 1923, 1924). In the case of the epithelium, these measurements are somewhat illusory, for while at certain stages the epithelial layer is clearly delimited against the underlying stroma, at other stages it is not, and therefore it is impossible to obtain definite values, though the measurements afforded valuable information for comparison.

During anestrus the amount of secretion is slight. The epithelium consists of columnar cells which, on the whole, form a level surface against the lumen of the tuba. As a rule the cell nuclei are somewhat elongated and basophilic. The epithelium is low, and ciliated cells are practically non-existent. The epithelial cells are chiefly of the intercalary or "peg-cell' type, (fig. 56).

During late pro-estrus and estrus, the lumen of the tuba is usually completely filled with secretion. The stroma of the mucosa is of loose consistency and is greatly vascularized, with dilatated vessels and large lymph spaces. Owing to the swelling of the stroma and the abundant secretion, the tuba, when slightly enlarged, gives the impression of being solid, especially in the ampulla and the cranial part of the isthmus. The epithelium is high and forms a smooth surface against the lumen of the tuba. As a rule a distinct basement membrane



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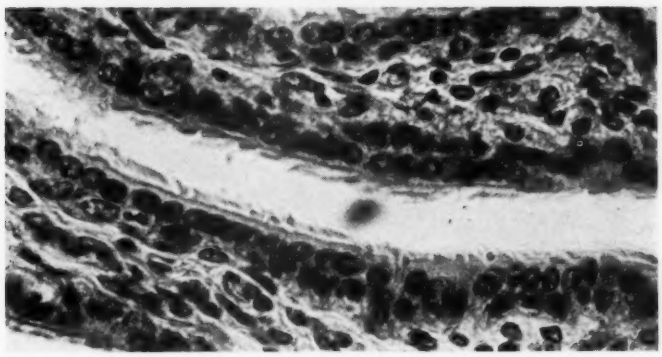

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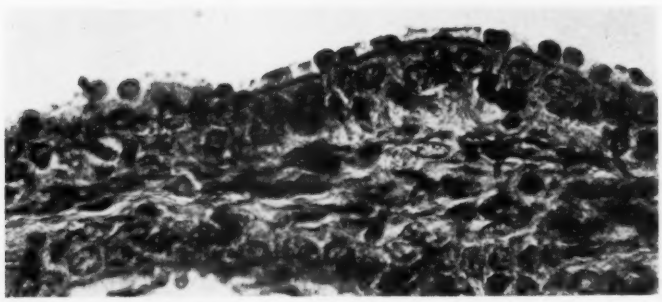


58

59

Figs. 56—59. Section through the mucosa in the ampulla: — 56. During anestrus. — 57. During estrus. Note the continuous border of cilia. — 58. During the passage of the eggs through the tuba. Note the secretion-droplets in the border of cilia. — 59. During pregnancy. (Hemalun-eosin stained, redfilter, 500 ×.)

can be observed between the epithelium and the stroma. With few exceptions the epithelial cells in the infundibulum and ampulla are ciliated, but in the isthmus, and especially against the tubo-uterine junction, ciliated cells are met with in whole colonies only in the crevices (cf. mice ALLEN 1922, AGDUHR 1927, and rats ALDEN 1942). In this stage the border of cilia is extremely beautiful, especially in the infundibulum and ampulla (fig. 57). It is remarkable that generally at this stage, in the case of secretion, no secretion-droplets or so-called balloon secretions are met with.

After ovulation significant changes take place in the tuba. The secretion is still abundant, but the lumen of the tuba is not so filled out with secretion as during estrus. This is partly due, however, to the stroma of the mucosa being less edematous than during estrus. The vessels are still strongly dilatated, and the whole tuba gives the impression of being extremely active. The ciliated cells gradually decrease in number, but during the passage of the egg through the tuba they are still met with in appreciable numbers. 'ESPINASSE (1935) observed that ciliated cells lost the cilia in connection with the secretion. It has been possible to make similar observations in mink too, and it appears probable that the decline in the number of ciliated cells is due to some such phenomena. During this period the epithelium reaches its greatest height, as is the case in pigs and man (SNYDER 1923, 1924), and in rats (ALDEN 1942). The secretion is of a different character from that met with during pro-estrus and estrus in that droplets, which are more stainable than other secretions, appear in relative abundance, (fig. 58). ALDEN (1942) considers that these droplets are fixation artefacts, and this may be correct if by that is meant that in the histological section their picture does not correspond to their picture *in vivo*. On the other hand, it is not correct if it is a question of their occurrence, for as they only appear during a definite phase of the sexual cycle, they must represent a genuine secretion process, the task of which is probably to supply the fertilized egg with nutriment.

During pro-estrus and estrus, and during the passage of the egg through the tuba, the tubas of females which are at the same stage exhibit identically the same picture. As soon as the eggs reach the uterus, this conformity ceases, and the changes run in two directions, independent of whether the eggs have been fertilized or not. In the majority of cases the epithelium resumes the estrous appearance, which implies that the secretion-droplets disappear, and the ciliated cells which have lost their cilia regenerate. In the females in which the development proceeds in this direction the corpora lutea are inactive. In very rare cases does the epithelium exhibit degenerative features. The ciliated cells disappear, and the epithelial cells are low, with long, dense, strongly basophilic nuclei. The surface of the epithelium is often uneven and recalls the picture which SNYDER (1924) found in the human being during di-estrus and pregnancy. The stroma of the mucosa appears dense, its vessels are constricted,

VOL.
28
194

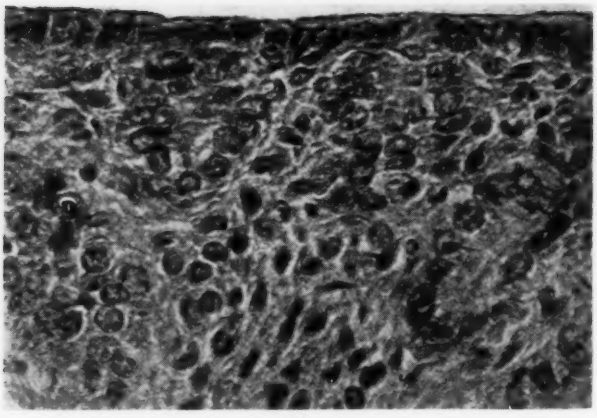
and the basement membrane is disintegrated. In this case, as far as can be judged, the corpora lutea are in an active incretion phase. This last-mentioned picture persists even during pseudo and genuine pregnancy (fig. 59).

The circumstance that the mink's tuba resumes its estrus character without going through the stage of degenerative changes in the form of nuclear and cell extrusions, reduced epithelial height and secretion, which have been proved in all the other animals studied (cf. ALLEN 1922, SNYDER 1923, 1924, 'ESPINASSE 1935, ALLEN, HISAW and GARDNER 1939, and ALDEN 1942), indicates that the female mink does not have several estrous cycles during the mating season. These divergencies in mink argue rather in favour of its having a long estrous period, which as a rule does not cease with, but is only modified by ovulation.

'ESPINASSE (1935) and ALDEN (1942), among others, have questioned whether it is justifiable to group the epithelial cells of the tuba into secretory, ciliated, and intercalary cells, for they consider that everything tends to indicate that this division has no real basis in fact. The study of the tuba in mink has confirmed this view. The circumstance that during anestrus the majority of the cells are of the intercalary type, ciliated during the pro-estrus and estrus, and secretory during the passage of the egg through the tuba, affords support for the assumption that these cells represent different stages of the same cells, rather than distinct and different types of cells.

3. UTERUS.

During the sexual cycle the uterus undergoes far-reaching changes, owing to changes in the activity of the endocrine glands. In a study of the reproduction in mink, owing to the variation in the length of the period between mating and implantation, especially the changes before implantation are of importance. In the earlier literature, however, mainly the decidual reactions in connection with implantation and the formation of the placenta were studied. These works could therefore be of very little service for judging the progestational proliferations in mink. In connection with the isolation of the hormone of the corpus luteum and the assays of this hormone, however, studies have been also made of the changes in the uterine mucosa during the preimplantation period (cf. CORNER and ALLEN 1929, ALLEN 1930 b, 1931, HISAW and LEONARD 1930, MCPHAIL 1934, PINCUS and WERTHESSEN 1937, and others). These works and those of ALLEN 1922, LONG and EVANS 1922, DEANESLY and PARKES 1931, LEONARD, HISAW and FEVOLD 1932, MARKEE 1932, ROBSON 1932, 1933, FOSTER and HISAW 1935, REYNOLDS and KAMINESTER 1936, LLOYD 1937, HECKEL and ALLEN 1937, GRANDALL 1938, LYON and ALLEN 1938, HOOKER 1940, KREHBIEL 1941 b, and in particular the detailed histological analysis of the changes in the uterine mucosa in cats by DAWSON



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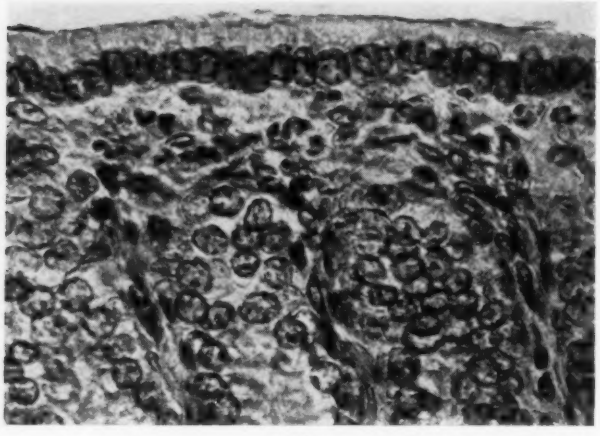


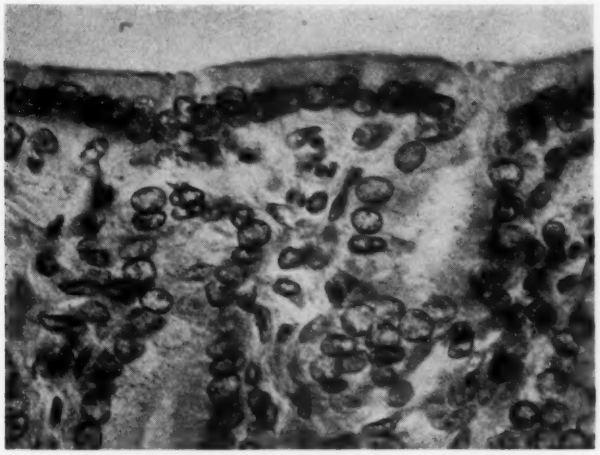
61

Figs. 60—61. Section through the uterus-mucosa: — 60. During anestrus. — 61. During estrus. (Hemalun-eosin stained, redfilter, 600 ×.)

and KOSTERS (1944) and in mice by HOOKER (1945), have been of assistance in the studies of the changes in the uterus of the female mink.

During anestrus the transverse section of the uterus has a more or less regular oval appearance. The vascular supply is slight, and the vessels are constricted. The muscularis and mucosa are low, and in the latter the diameters of the glands are inconsiderable. The secretion cells are low, with basally situated cell nuclei. Owing to the inconsiderable lumina of the uterine glands, the surface epithelium appears to be continuous and forms a layer which is, on the whole, compact (fig. 60).

During pro-estrus and on to estrus, the uterus increases greatly in size. This growth is due partly to the increased vascularization and dilatation of the ves-



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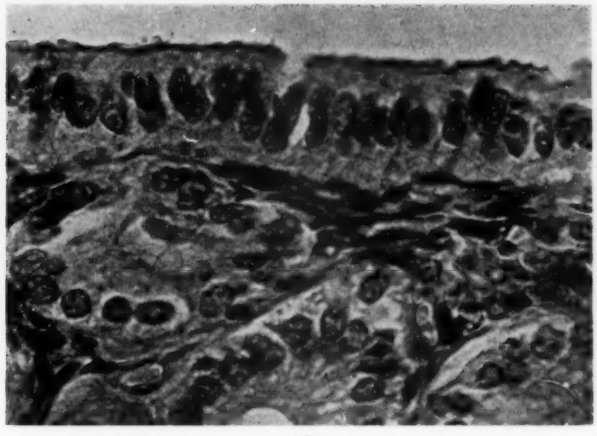

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Figs. 62—63. Section through the uterus-mucosa: — 62. During the free-vesicle stage. — 63. During the onset of implantation. (Hemalun-eosin stained, redfilter, 600 ×.)

sels, which leads to an increased accumulation of fluid in the tissues, and partly to mitotic activity in the latter. These changes proceed continuously up to the time of estrus. At that time both the muscularis and the mucosa are greatly thickened. In the mucosa the uterine glands especially are greatly developed, firstly by means of cell division in the gland epithelium, and secondly owing to an increase in the volume of the individual cells. Their lumina are enlarged, so that the surface epithelium no longer appears to be continuous. The cells in the latter are also considerably higher than previously, but both in the glandular and in the surface epithelium the nuclei are still situated basally (fig. 61).

DAWSON and KOSTERS (1944) were able to show clear changes in the uterine glands in cats 48 hours after they had been mated, and in the surface epithelium after 96 hours. These changes showed themselves in the form of mitotic activity, especially of the glandular epithelium, and of deposits of glycogen in the glandular cells, and in the surface epithelial cells, the nuclei of these cells being apically displaced. In cats the deposits of glycogen reach their maximum on the seventh day after mating. At that time the uterine glands dilate greatly towards the uterine lumen. As a result of this, the luminal surface has a fringed or hillocky appearance. In assays of progesterone progestational proliferations are not spoken of before this latest stage.

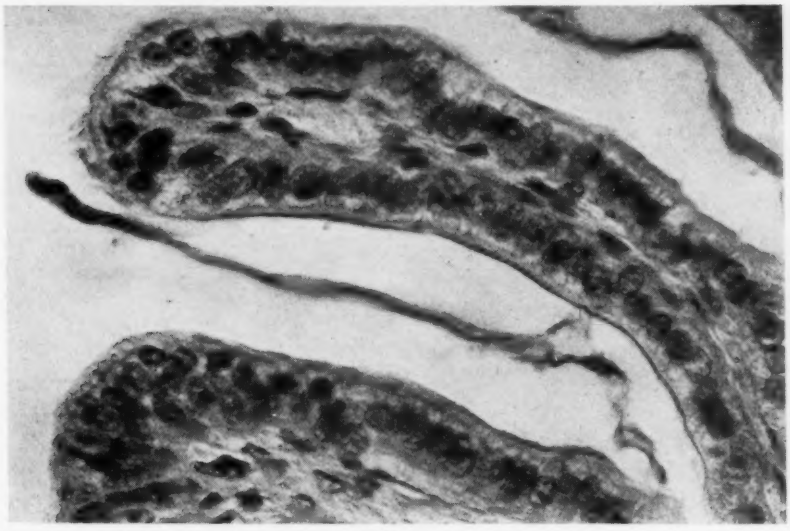
In mink, after they have ovulated and during the free vesicle stage, no tendency towards increased deposits of glycogen or an apical displacement of the cell nuclei in the glandular and surface epithelium can be traced. Nor can any such intracellular edema be recognised as HOOKER (1945) found in mice, as a result of progesterone injections (fig. 62). Not until the blastula, when flushed out, shows a tendency to adhere to the mucosa do we meet with maximum deposits of glycogen, apically displaced nuclei, and commencing fringing of the luminal surface (fig. 63).

The further development of the uterine mucosa is dependent on whether blastulae are present in the uterine lumen or not. If there are no blastulae, the fringing of the luminal surface continues, and the large folds in the mucosa become typically tree-shaped in appearance, owing to the enormously enlarged lumina of the glands (fig. 65). At this stage the whole mucosa constitutes a greatly ramified supporting tissue, in the fibres of which vessels and nerves ramify. These connective tissue fibres are usually coated with a single layer of high cylindrical epithelial cells. As can be seen by comparing fig. 65 with fig. 64, the uterine-mucosa of pseudo-pregnancy resembles that of early pregnancy. The length of the pseudo-pregnant condition appears to be considerable. Thus 40 days after the mating no signs can be traced of regeneration of the mucosa.

4. VAGINAL CONTENTS.

After STOCKARD and PAPANICOLAOU (1917) had shown on the guinea-pig that these changes in the vaginal epithelium which are correlated with the estrous cycle could be followed by means of studies of the cellular structure of the vaginal smear, this method was employed in a very large number of investigations, partly to study the estrous cycle (LONG and EVANS 1922, ALLEN 1922, SELLE 1922, HAMMOND 1927, KUNDE and PROUD 1929, TINKLEPAUGH and CAMPENHAUT 1931, PAPANICOLAOU 1933, GRANT 1934, YOUNG, MYERS and JENNISON 1934, FOSTER and HISAW 1935, YOUNG 1937, GRIFFITH and AMOROSO 1939, JOHANSSON 1941, etc.), and partly as a method of assaying the ovarian hormone (ALLEN and DOISY 1923, KAHNT and DOISY 1928).

VOL
28
194



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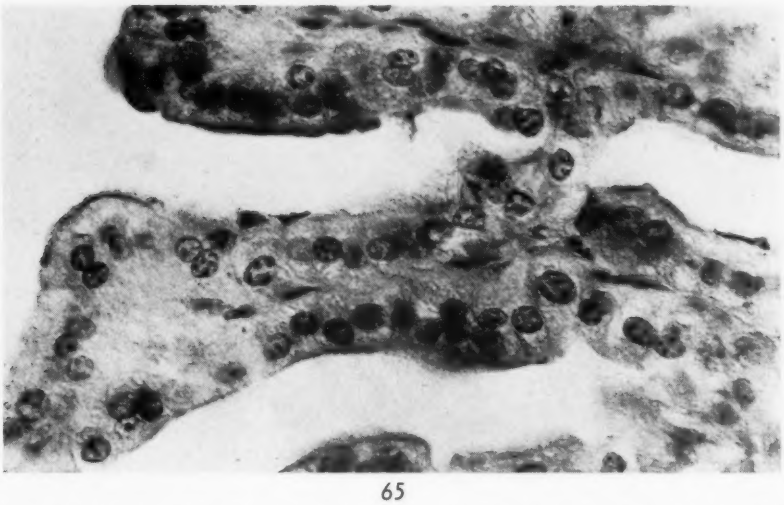


65

Figs. 64—65. Section through the uterine mucosa: — 64. Showing the fringing of the mucosa in early implantation. Note the ingrowths of the blastodermic vesicle. — 65. Showing the fringing of the mucosa in early pseudopregnancy. (Hemalun-eosin stained, red-filter, 600 ×.)

The vaginal smear tests have the advantage over studies of the vaginal epithelium after autopsy that the changes can be followed during an unlimited period. It has, however, certain weaknesses which must not be overlooked. WADE and DOISY (1935) and EMERY and SCHWABE (1936) have shown that especially the cotton swab method frequently results in positive estrus-like

smears, if smears are taken daily or more frequently. This source of error can be avoided by only taking vaginal secretion specimens every other day, and then not using the cotton swab method. GRANT (1934) pointed out that, as regards time, the vaginal secretion test does not give a true picture of the vaginal epithelium in sheep, for the cells in the secretion may have been delaminated off at an earlier point of time but have remained in the vaginal lumen. This source of error asserts itself especially in animals with a cyclical vaginal secretion, as in the case of sheep and cows; but in, e.g., the mink, where the vaginal secretion is never very large, it plays a less important rôle. A method which combines the advantages of autopsy with those of the vaginal secretion test was employed by DAWIS and HARTMAN (1935), namely frequent biopsies in the vagina. This method, which is very effective with larger animals, cannot be employed on mink for any considerable time, owing to the small size of the vagina.

The studies of the vaginal epithelium in mink were chiefly carried out indirectly by taking specimens of vaginal secretions. In some cases the vagina was histologically elaborated after autopsy in order to verify the vaginal secretion tests. To avoid the artificial production of estrus-like smears, the specimens were taken with a silver loop and not more frequently than every other day. A smear preparation was made of each specimen, fixed in alcohol, stained with eosin and hemalun, and mounted in Canada balsam. As appears from table 30, 1,507 vaginal secretion specimens were taken, which are distributed over 6 different months, all the sexual stages being represented.

Table 30. *Distribution of specimens of vaginal smears over different months.*

Months	Number of smears
September	10
November	24
Januari	59
February	369
March	926
April	119
Total	1507

The vaginal secretion in mink is extremely inconsiderable, even during estrus, and the comparisons of the specimens were therefore made exclusively on the basis of the structure of the smear cells, which may be divided into the following components:

1. Vaginal epithelial cells, small, rounded, with clearly stainable nuclei and seemingly healthy.

2. Vaginal epithelial cells, large, irregular and cornified with more or less visible nuclei.

3. Vaginal epithelial cells, small, autolysed, with clearly stainable nuclei.

4. Leukocytes, mainly polymorphonuclear.

5. Cell detritus of various kinds.

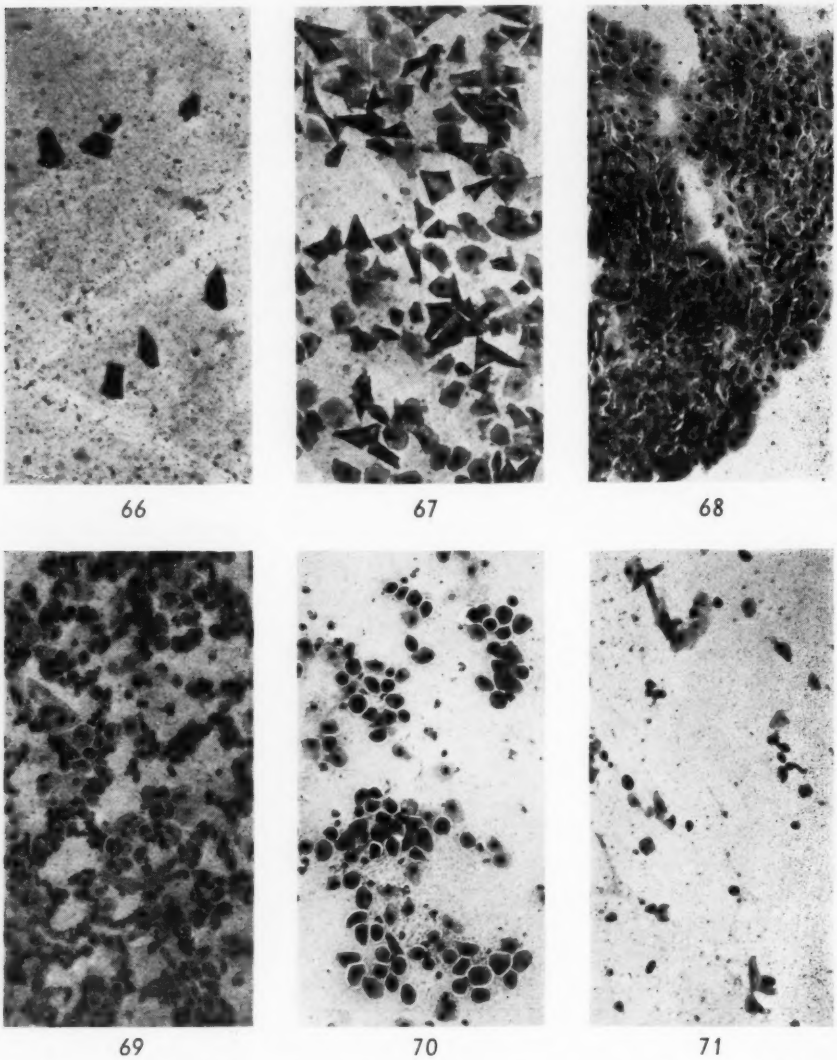
Furthermore, there is the desquamation of massive character, in which several layers of more or less cornified cells are cast off synchronously from the vaginal surface.

During September and November, when the female mink is in anestrus, there is extremely little secretion in the vagina. The components consist of occasional autolysed epithelial cells, leukocytes and various cell detritus, and in extremely rare cases of cornified cells with clearly visible nuclei.

At the end of January this anestrus stage passes gradually into the pro-estrus stage. The vaginal secretion, including the delamination of cells, increases, and among the components rather large, more or less cornified irregular epithelial cells predominate (fig. 66). Autolysed small epithelial cells and miscellaneous cell detritus are met with sparsely, but leukocytes extremely rarely. During the pro-estrus and on to the estrus, the vaginal secretion changes, the large irregularly shaped epithelial cells becoming more cornified and larger, but at the same time thinner, and owing to this they have a characteristic tendency to roll up at their corners in the preparation (fig. 67). Some days before estrus, a tendency can also be proved in the majority of cases towards an increased secretion of mucus. The changes in the vaginal secretion during pro-estrus take place so slowly that no definite changes can be proved in the course of a few days. ENDERS (1939 a) considers that in mink he found clear changes from two days before mating up to the mating. In view of the large number of secretion specimens which were studied during this interval in the present author's investigations and the results obtained, ENDERS' results do not appear to be generally applicable.

Immediately after copulation, the vaginal secretion contains abundant sperms and secretion originating from the semen. On the other hand, there are extremely few cells from the vaginal epithelium, and it seems as though the act of mating had entirely emptied the vagina of its own secretion.

After ovulation a marked tendency is found towards an increase in the cornified irregular epithelial cells, which often appear in whole colonies. As far as can be judged, these correspond to the "cheesy mass" of STOCKARD and PAPANICOLAOU (1917) and to the massive desquamation or delamination of epithelial cells described by several other authors. A remarkable circumstance is, however, that, in the other animals examined, the desquamation process is followed by a heavy infiltration of leukocytes into the vaginal epithelium, which also penetrate into the lumen and consequently appear in the secretion.



Figs. 66—71. The vaginal contents during: — 66. Proestrus. — 67. Estrus. — 68. Final desquamation. — 69. Leukocytic invasion. — 70. After the leukocytic invasion. — 71. During gravidity. (Hemalun-eosin stained, greenfilter, 100 ×.)

This is not the case in mink, in which only masses of more or less cornified epithelial cells, which remain for some days, are met with, after which their number diminishes, and the secretion again assumes the estrus character. Thus six to seven days after mating, all the females, with very few exceptions, exhibit the estrous picture. In the cases where the female is not mated again, this stage persists for a longer or shorter period, independently of whether the

female is pregnant or not. This estrous stage has its counterpart in the ovary in the inactive phase of the corpora lutea, and in the tuba and uterus in a more or less clear estrous picture. Thus the adnexal organs exhibit complete agreement, which is not surprising, for, as ALLEN (1922) says, "The oviduct, uterus and vagina have a common origin from the mullerian ducts, so possibly factors causing cyclic changes in the uterus and vagina may be expressed in some way in the oviducts".

As the prelude to the final disappearance of the estrous picture, a violent increase takes place in the cornified cells in the smear, which appear in whole colonies, and a definite desquamation of the cornified layer takes place (fig. 68). This is followed by a heavy infiltration and invasion of polymorphonuclear leukocytes (fig. 69). At the same time numerous, small, rounded, healthy epithelial cells appear in the smear (figs. 69 and 70). During pregnancy the vaginal secretion contents resemble those during anestrus. The components consist of autolysed epithelial cells, miscellaneous cell detritus, and a few cornified epithelial cells (fig. 71).

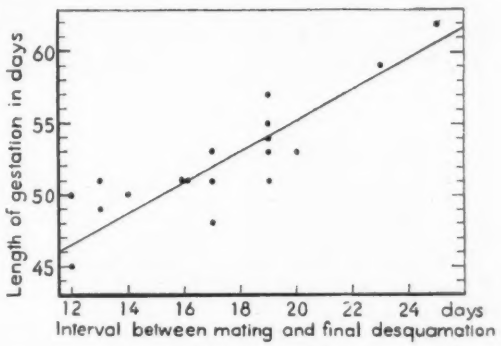


Fig. 72. Length of the interval between mating and final desquamation in relation to the length of gestation in 19 females.

In order to investigate the relation between the final desquamation and implantation, a number of females were studied by means of vaginal secretion tests every other day from the time of mating until the final desquamation took place. Of the females 19 gave birth to cubs. In these 19 females both the length of the interval between mating and the final desquamation and the length of the gestation period could be estimated. However, it proved none too easy to determine exactly the onset of desquamation, partly because this process begins more abruptly in certain females than in others, and partly because the tests were made only every other day. The point of time of desquamation was taken to be the first appearance in the vaginal secretion of considerable numbers of leukocytes. In fig. 72 is shown the relation of the length of the interval between mating and the final desquamation to the length of the gestation period. A calculation of the coefficient of correlation gave the figure 0.918***, and the coefficient of regression reached the value 1.079. Thus the time of onset of the final desquamation must be intimately related to the renewed activity in the corpora lutea and to the onset of implantation.

By way of summary, it may be said that the changes in the vaginal secretion in mink conform entirely with conditions in other animals up to the estrus.

Owing to the long pro-estrus period, however, the changes from anestrus to estrus take place very slowly, and therefore as a rule they are not perceptible for a couple of days. After ovulation, only a partial desquamation of the cornified layer follows, and no invasion by leukocytes takes place. It does not appear correct, therefore, to speak of several estrous cycles in mink, for there is no metestrous stage, as there is, e.g., in rats and mice (LONG and EVANS 1922, ALLEN 1922). The partial desquamation will probably be due to a violent follicular increase, owing to copulation, and continues up to the time of ovulation, which is probably accompanied by an increased incretion of estrogen. When ovulation takes place, the estrogen content of the blood falls suddenly, and this gives rise to the partial desquamation. The latter is interrupted by a further follicular increase and consequently by a fresh increase in the incretion of estrogen. This is also confirmed by the fact that, if mating does not take place, no cyclical change, with desquamation in the vaginal secretion, is met with. In connection with the renewed activity in corpora lutea which occurs immediately before implantation, a final desquamation takes place.

VOL.
28
194

E. INTERNAL FACTORS IN DELAYED IMPLANTATION.

In the preceding section it was shown that, in the ovaries and in the tuba, uterus and vagina, the delayed implantation leads to significant changes in the histological picture. With the guidance of this, and bearing in mind the mating conditions, the dependence of the length of gestation on the date of mating and the ovulation conditions, the variation in the embryonic development and the endocrine interplay between the sexual hormones, the following experiments were carried out, in an endeavour to elucidate the underlying causes of the delayed implantation in mink.

1. Administration of progesterone with and without estrogen to mated normal and ovariectomized females.

2. Administration of estrogen in connection with mating.

3. Administration of gonadotropic substances of urine and blood serum to mated females.

The hormone preparations employed in these experiments were the following: Progesterone: Lutex S Leo and Progestin. Estrogen: Menformon and Ovex Leo. Extract of pregnancy urine (PU): Physex Leo and Pregnyl. Extract of blood serum of pregnant mares (PMS): Gestyl and Antex Leo. In all cases the injections were given intramuscularly and alternately in the femoral musculature of the hind extremities.

The females were only permitted one mating, and all attempts at mating were carefully controlled. For the purpose of judging of the effects of the injections, firstly the vaginal secretion was examined at two-day intervals,

secondly the length of gestation for the females were compared with an expected length calculated in the same way as in table 27, p. 80 and thirdly, autopsies were performed on some of the females.

1. ADMINISTRATION OF PROGESTERONE WITH AND WITHOUT SIMULTANEOUS ADMINISTRATION OF SMALL AMOUNTS OF ESTROGEN TO MATED, NORMAL AND OVARIECTOMIZED FEMALES.

The histological picture of the corpora lutea during the free vesicle stage, and also the circumstance that the female exhibits estrus, permits mating, and ovulates during that period, indicate a deficient secretion of progesterone. This is also confirmed by the histological picture of the tuba, uterus and vaginal secretion. As WEICHERT (1939, 1940) considered that he could prove that the injection of progesterone into lactating rats promoted implantation, similar experiments were made on mink, in spite of the fact that HAMLETT (1935), PINCUS (1936) and SELEY (1939) arrived at negative results in the case of corresponding injections into the nine-banded armadillo and mice.

As in a series of investigations (cf. WESTMAN and JACOBSOHN 1937 a, b, c, HISAW, GREEP and FEVOLD 1937, ROBSON 1937 c, 1940, and JOST 1939, ROTCHILD, MEYER and SPIELMAN 1940, MERCKEL and NELSON 1940, and GILLMAN and STEIN 1942) it was shown that estrogen in small quantities has a synergistic effect on progesterone, a series of experiments was carried out with injections of progesterone, in which small amounts of estrogen were given at the same time. The amount of progesterone injected and the size of the injections, in relation to the interval after mating, were varied widely. This is shown to some extent in table 31. Certain females received up to 5.00 mg of progesterone in one injection, and others 9.00 mg during the course of 6 days.

As appears from table 31, the 4 females which were given 80 IU of estrogen and 0.95 mg of progesterone had a gestation period which was 2.9 days shorter than had been expected. As in these cases the females were given the proge-

Table 31. *Influence of combined injections of progesterone and estrogen on length of gestation.*

Total amount of injected hormones		Number of females		Number of cubs per female	Mean length of gestation		
estrogen, I.U.	progesterone, mg	total	pregnant		actual	expected	difference
80	0.95	4	2	2.25	50.0	52.9	— 2.9
25	1.00—4.00	8[1]	4	3.17	52.8	51.4	+ 1.4
475—950	13.00	6[2]	4	3.80	52.8	53.1	— 0.3
	Total and mean	18	10	3.13	52.2	52.4	— 0.2

[1] Two females autopsied. [2] One female autopsied.

sterone distributed over 5 injections 2—10 days after mating, and as the implantation took place 16 days after mating at the earliest, it is not probable that the injections affected the implantation. The discrepancy was probably entirely due to chance.

In the other two experimental groups the hormones were given by means of injections every day and every other day respectively, from the 4th up to the 25th day after mating. As appears from the table, there is no appreciable difference in the actual and the expected length of the gestation period, and thus the injections did not affect implantation. Nor did a study of the vaginal secretion reveal any effect from the injections. The character of estrus persisted, in spite of the injections of progesterone, nor was the time for the final desquamation of the cornified layer and the massive infiltration of leukocytes affected. Nor could any effect from the injections be traced at the autopsies on three females made in association with the experiment. Both the tuba and the uterus exhibited the estrous picture. The latter was turgid, with strongly dilated vessels and large lymph sinuses. Both the surface epithelium and the epithelium in the uterine glands exhibited the typical estrous character. This negative result will probably not be due to the amounts of progesterone supplied having been too small, for HISAW, GREEP and FEVOLD (1937) obtained fully developed progestational reactions even with the administration of 1.00 mg of progesterone daily to ovariectomized rabbits, and PINCUS and WERTHESSEN (1938) obtained normal implantation and pregnancy with the administration of the same amount of progesterone daily to ovariectomized rabbits, as was confirmed by JOST (1939) and COURRIER and JOST (1939). HISAW and GREEP (1936) showed that 0.50 mg of progesterone daily, together with 25—200 RU of estrogen, led to a clear progestational proliferation in castrated monkeys after 19—32 days. As both rabbits and monkeys are considerably larger than mink, it might be expected that smaller amounts of progesterone would lead to progestational reactions in mink. The negative result, therefore, indicates rather that the effect of the progesterone was suppressed. As HISAW and LEONARD (1930), ALLEN (1932), and LEONARD, HISAW and FEVOLD (1932), showed that, in considerable amounts, estrogen has a marked antagonistic effect as against progesterone, it readily suggest itself to assume that the injected estrogen, or the estrogen increted by the ovaries suppressed the effect of the progesterone. To investigate this question an experiment was carried out with injections of progesterone only. The experiment was made on 30 females, and the amount of hormone injected was varied in the same way as in previous experiments.

As appears from table 32, the females which were given the smallest amount of progesterone exhibited gestation periods which were shorter by 3.1 days than had been expected. As these females, like the corresponding ones in table 31, were given progesterone distributed over 5 injections 2—10 days after

VOL
28
194

Table 32. *Influence of injections of synthetic progesterone on length of gestation.*

Total amount of injected progesterone in mg	Number of females		Number of cubs per female	Mean length of gestation		
	total	pregnant		actual	expected	difference
0.95	4	3	2.25	49.3	52.4	— 3.1
5.20	10	9	3.50	58.0	57.8	+ 0.2
8.00—9.75	10[1]	6	3.75	53.0	50.8	+ 2.2
10.50—13.25	6	5	3.00	54.6	50.7	+ 3.9
Total and mean	30	23	3.29	54.8	53.7	+ 1.1

[1] Two females autopsied.

mating, and as implantation took place at the earliest 15 days after mating, it does not appear probable that the injections affected the implantation. In the other three groups which were given progesterone injections every day and every other day respectively from the 4th to the 25th day after mating, the gestation period was somewhat longer throughout than had been expected. A similar protraction of gestation was also found in experiments with lactating mice, (PINCUS 1936). Thus the administration of progesterone alone did not promote implantation. Nor did a study of the picture of the vaginal secretion reveal any effect due to the injections of progesterone, for the cornified epithelial cells remained even after the injections, and the time of the final desquamation was not affected. Nor did the histological picture of the tuba and uterus of the two females which were killed in association with the experiment, exhibit any progestational reaction as a result of the treatment.

As the amounts of progesterone administrated should in themselves have been sufficient to cause a decidual reaction, the question arises whether the negative result may be due to the synthetic progesterone not being fully equivalent to the estrogen-free incretion substances in the corpora lutea. However, investigations by CORNER (1937), PHILLIPS (1937), MAKEPEACE, WEINSTEIN and FRIEDMAN (1937), HECKEL and ALLEN (1937), LLOYD (1937), PINCUS and WERTHESSEN (1938), PHILLIPS and YOUNG (1938), ALLEN and HECKEL (1939), JOST (1939), COURRIER and JOST (1939), HOOKER (1940), MØLLER-CHRISTENSEN and FØNSS-BECH (1941), showed that synthetic progesterone, like extract of corpus luteum, has the capacity of suppressing estrus, giving rise to progestational proliferation, rendering implantation possible, and maintaining pregnancy. It does not therefore seem probable that the negative result is due to qualitative differences between the synthetic progesterone and the estrogen-free incretion substances of the corpora lutea.

As has been repeatedly pointed out, during the free vesicle stage the female exhibits the estrous picture in the tuba, uterus and vaginal secretion, in her willingness to mate, and in ovulation. This indicates an active estrogen incretion,

and as estrogen in considerable amounts has an antagonistic effect on the progesterone, it readily suggests itself to assume that it is this estrogen incretion which prevents implantation, even in the cases where the supply of progesterone has been administrated by means of injections. COURRIER and GROS (1932, 1935) also showed that in cats implantation can easily be prevented by means of injections of estrogen. If this assumption is correct, it should be possible to cause progestational reactions and possibly implantation in mink by first eliminating the incretion of estrogen and then supplying progesterone.

For the purpose of investigating this question, ovariectomy was performed in 1946 on 5 mated females, immediately before or immediately after the time when it was calculated that the fertilized egg would pass down into the uterus. In order to avoid damaging the fur unnecessarily, the ectomization was performed through a short incision in the linea alba. This operation technique was unfortunate, however, for the females operated upon showed an inclination to gnaw through the sutures, which led to the death of three females before the autopsies should have taken place in accordance with the experimental plan. If the incision had been made dorsally, this might have been prevented.

One of the females was ectomized 9 days after mating and was subsequently given 2.00 mg of progesterone daily in two injections. An autopsy was made after 76 hours. The uterus had then lost the turgidity typical of estrus. The histological examination confirmed this observation, but on the other hand no marked effect of the injections of progesterone could be traced. The glycogen storage in the surface and glandular epithelium was not especially striking, and no fringing of the surface epithelium could be observed. The result shows, however, that the ovaries have an active incretion of estrogen during the free vesicle stage, for ovariectomization leads to a regressive estrous phase in the uterine mucosa.

One of the females was ectomized 6 days after mating and was subsequently given, firstly, 1.00 mg of progesterone daily in two injections, and secondly, 20 IU of estrogen on the 1st and 4th days after the ectomization. An autopsy was performed 7 days after the operation. When the right uterus horn was flushed out, 4 blastodermic vesicles were found, in which the degree of development corresponded to that shown in fig. 38. They exhibited the same tendency to adhere to the uterine mucosa and the same tendency to shrivel as was shown in section VI to be the case with commencing implantation. The turgidity of the uterus had disappeared, and in the surface and glandular epithelium glycogen had been deposited in such a way that the cell nuclei were apically displaced. In the lumen of the uterine glands there was also abundant secretion. The necks of the uterine glands were so distended that a commencing fringing of the surface epithelium could be observed. This shows both that ovariectomization resulted in the elimination of an active incretion of estrogen

VOL 28 194

and that, after the elimination, a supply of synthetic progesterone may give rise to such decidual reactions that implantation can begin.

The experiments carried out thus showed that a supply of progesterone, with or without a simultaneous supply of small amounts of estrogen, to normal mated females during the free vesicle stage does not affect the uterus or implantation, for the incretion of estrogen which takes place in the ovaries during this phase suppresses the effect of the progesterone. If this incretion of estrogen is eliminated, the progesterone injections lead to decidual reactions. The delayed implantation in mink is thus dependent on a continued active follicular phase during the free vesicle stage.

2. ADMINISTRATION OF ESTROGEN TO NORMAL MATED FEMALES.

It is probable that the active follicular phase in the ovaries during the free vesicle stage does not depend on the ovaries themselves, but that it is regulated by the anterior pituitary. Administration of estrogen has proved to check the formation of, or the release of, follicle-stimulating substances from the anterior pituitary (cf. WITSCHI and PFEIFFER 1935, DEMPSEY 1937, FEVOLD 1939 a, b, MERCKEL and NELSON 1940, and ASTWOOD 1941). Similarly, investigations have shown that estrogen is necessary for the normal development and functioning of the corpora lutea (cf. WESTMAN and JACOBSOHN 1937 a, b, c, ROBSON 1937, 1940, and JOST 1939). It is, then, conceivable that the estrogen incretion in connection with ovulation is not sufficient to affect the hypophysis, so that the latter ceases to stimulate follicular growth, and that as a result the development of the corpora lutea cannot take place normally. Experiments were therefore made to raise the estrogen level at the time of mating by the injection of estrogen, in the hope of thereby inducing the hypophysis to discontinue the release of follicle-stimulating hormone.

The experiment was carried out on 13 females and, as shown in table 33, the amount of estrogen injected varied from 100—1,500 IU. In the first group

Table 33. *Influence of estrogen injections on length of gestation.*

Total amount of injected estrogen in I. U.	Number of females		Number of cubs per female	Mean length of gestation		
	total	pregnant		actual	expected	difference
100 before mating	4	4	6.75	53.0	52.7	+ 0.3
500 at „	3	1	2.33	51.0	51.9	— 0.9
1,000 „ „	3[1]	2	2.50	55.5	52.8	+ 2.7
1,500 „ „	3	1	0.33	60.0	51.9	+ 8.1
Total and mean	13	8	3.33	54.3	52.5	+ 1.8

[1] One female autopsied.

the estrogen injections were given on the days before the mating. The length of gestation for these females was normal, and the fertility even very good. Manifestly the injections had no effect on the length of gestation. In the other three groups the injections were given immediately after the matings, for it proved difficult to induce mating in association with previous injections. As appears from table 33, the gestation period increases both absolutely and relatively to the expected gestation period. The smallness of the number of fertile females precludes any definite conclusions, but the results may possibly be interpreted as indicating a tendency for the large estrogen injections further to delay implantation. In this case autopsy was carried out on only one female, but the histological picture and the studies of the vaginal secretion only showed a persisting estrous condition.

The low fertility exhibited by the last three groups is worthy of notice. It seems probable that it is mainly due to the estrogen injections having temporarily had a checking effect on the release of follicle-stimulating hormone from the anterior pituitary, which resulted in the number of ovulated follicles being reduced (cf. page 51).

VOL
28
194

3. ADMINISTRATION OF GONADOTROPIC SUBSTANCES OF URINE (PU) AND BLOOD SERUM (PMS) TO NORMAL MATED FEMALES.

WEICHERT'S (1939, 1940) positive results from the treatment of lactating rats with gonadotropic substances of pregnancy urine led to experiments with gonadotropic substances on mink also. In the present author's unpublished investigations it is shown that the female mink can be brought to ovulate by the injection of PU and PMS. With the object of preventing this effect, the injections were only given during the first four days after mating, i.e., during the refractory stage in ovulation (cf. page 46).

The experiment was carried out on three groups, each of 8 females. One group was given PU, one PMS, and one equal parts of PU and PMS. Each group was divided into 4 sub-groups, three of which were given 150, 450 and 700 IU of hormones respectively, distributed over 5 injections, and one group 600 IU of hormone in 2 injections. As there were no appreciable differences in the results as between the different sub-groups, the latter have been thrown together in table 34.

As appears from this table, all the groups exhibited very low fertility. This is particularly true of the females which were given injections of PMS. Only one of them gave birth at all, and then to one cub, which was stillborn. An autopsy on one female in this group, 8 days after mating, revealed ovaries exhibiting numerous vesicular follicles, whose theca interna had proliferated and penetrated into the antrum folliculi. This characteristic thecal luteinization appears to tally exactly with what was found by SELEY, COLLIP and THOMSON

Table 34. *Influence of injections of the gonadotropic substances P. U. and P. M. S. on length of gestation.*

Total amount of injected hormones in I. U.		Number of females		Number of cubs per female[4]	Mean length of gestation		
P. U.	P. M. S.	total	pregnant		actual	expected	difference
—	150—700	8[1]	1[2]	—	(57)	50.2	(+ 6.8)
150—700	—	8[1]	4	2.43	51.5	50.9	+ 0.6
75—350	75—350	8[1]	4[3]	0.71	55.3	52.6	+ 2.7
	Total and mean	24	9	1.05	53.8	51.6	+ 2.2

[1] One female autopsied. [2] Only still-born cubs. [3] Only still-born cubs in two females. [4] Calculated only on living cubs.

(1934) in rats after the injection of gonadotropic substances. The uterine mucosa in this female exhibited a hyperestrous reaction, with an enormous accumulation of fluid.

Two of the females which received PU gave birth to normal litters, in two cases only one cub was born, and the remainder had no cubs. The injection of PU, too, led to an abnormal accumulation of fluid in the uterine mucosa, and the theca interna of the vesicular follicles had proliferated. When PU was injected, however, the changes were not so pronounced as when the females received PMS.

The group which were given equal parts of PU and PMS were intermediate between the two preceding groups, as regards both fertility and the changes in the ovaries and uterus.

As appears from the table, the injections tended to prolong gestation instead of shortening it. Thus this result is entirely contrary to that reached by WEICHERT (1939, 1940), but fully tallies with the results obtained by TEEL (1926), HAIN (1932, 1934), SNYDER (1934), HOOPER and KING (1935) and KING (1938).

F. DISCUSSION.

The experimental investigations have shown that the great variations in the length of gestation of the female mink is due to the circumstance that, after its passage through the tuba, the blastula enters into a phase of relative rest, which varies in length. This gives rise to a question of very great importance in principle, namely whether this stage of rest is due to the blastula itself, or to the fact that the uterine mucosa is not ready for placentation. BRAMBELL (1937) considered that the delayed implantation might be due to the cessation of the development of the blastula before the implantation stage, and that this in its turn might be due to an insufficient incretion of growth-stimulating

substances. On the other hand, according to BRAMBELL, even during the free vesicle stage, the uterine mucosa is prepared for placentation. BRAMBELL finds support for his view in the conditions in rats, in which animals, as has been mentioned earlier, traumatization of the uterine mucosa leads to decidual reactions, even during the free vesicle stage. This hypothesis of BRAMBELL's cannot be summarily dismissed, even though the investigations made by TEEL (1926), LYON and ALLEN (1938) and KREHBIEL (1941) indicate that the uterine mucosa in rats is less sensitive to traumatization during the free vesicle stage than during implantation. Therefore, with the conditions met with in mink as the starting-point, BRAMBELL's hypothesis will be further discussed.

If, as BRAMBELL pre-supposes, the delayed implantation depends only upon the degree of development of the blastula, in the case of the female mink this must mean that blastulae ready for implantation also constitute a pre-condition for the progestational proliferations in the uterine mucosa, for, as has been shown previously, during the free vesicle stage no such changes can be shown in the uterine mucosa. But typical pseudo-pregnancy, with pronounced changes in the uterine mucosa, is found in females whose ovulation has been elicited by riding by the males. Thus, in this case, the decidual reaction was elicited, although no eggs were fertilized. This shows that in mink, as in cats, ferrets, rabbits, etc., the decidual reactions are not dependent on whether blastulae ready for implantation are present in the uterus. This is the first evidence against the correctness of BRAMBELL's hypothesis. But, further, in mink the development of the blastula appears never to cease entirely during the free vesicle stage (cf. section VI). For this reason, in cases of greatly delayed implantation, blastulae are found which are appreciably further developed, although implantation has not commenced, than are the blastulae whose implantation commenced a short time after the mating. This does not indicate that the degree of development of the blastulae conditions the delay in implantation. Furthermore, during the resting stage of the blastula, the female exhibits estrus, permits mating and ovulates. During the same phase there is a more or less pronounced estrous condition in the tuba, cornua uteri and vagina, and the corpora lutea exhibit an inactive picture. This circumstance constitutes a further strong argument against the correctness of BRAMBELL's hypothesis, at least where the delayed implantation in mink is concerned, for otherwise the female's estrous condition shold not be affected. In all probability it will therefore be possible to say that the delayed implantation is not due to retarded embryonic development, but to the fact that the uterine mucosa is not ready for implantation. The fact that the development of the blastula ceases, may, of course, conceivably be due to the incretion of possible growth-stimulating substances exhibiting co-variation with the incretion of the endocrine substances which regulate the reaction of the uterine mucosa. On

the other hand, it appears more probable that the retardation of embryonic development is due simply to the delayed placentation.

During the stage of relative rest of the blastula, the female exhibits estrus, permits mating and ovulates, as is shown by the experimental investigations. During the same stage there is a more or less pronounced estrous condition in the tuba, uterus and vagina, at the same time as the corpora lutea exhibit an inactive picture. During this stage supplies of progesterone of up to 5.00 mg per day, with or without a simultaneous supply of small amounts of estrogen, have no perceptible effect on the female's estrous condition or on the uterus and implantation. On the other hand, the contrary is the case if ovariectomy is first performed. The estrous condition then ceases, progestational proliferations begin in the uterine mucosa, and implantation is promoted. All this together is very strong evidence that during the free vesicle stage there is such a change in the incretion of estrogen and progesterone in the ovaries that the changes in the uterine mucosa necessary for the placentation cannot take place, and this prevents the implantation of the blastula.

Irradiation experiments on mink and marten have shown that light hastens implantation. As has been mentioned earlier, light affects the sexual functions by way of the hypophysis. This indicates that the change in the incretion of estrogen and progesterone in the ovaries during the free vesicle stage may, in its turn, be dependent on a corresponding change in the incretion of gonadotropic substances in the anterior pituitary

In a discussion of the underlying causes of the delayed implantation, therefore, the complicated and still not fully elucidated interplay between the anterior pituitary and the ovaries must also be dealt with. In view of the numerous investigations which have been carried out in this field, it is impossible to discuss this problem in detail without referring to the detailed surveys given by SMITH (1939) and FEVOLD (1939 b).

By means of hypophysectomy and severance of the stalk of the hypophysis in various animals and at different sexual stages, it has been shown in a large number of experiments that the anterior pituitary intimately regulates the activities of the ovaries. Hypophysectomy alone cannot, however, render possible a detailed analysis of the relation between the anterior pituitary and the ovaries, for at the same time all the substances in the anterior pituitary which possibly affect the ovaries are eliminated. Since FEVOLD, HISAW and LEONARD (1931) succeeded in isolating two different substances with gonadotropic effects from the anterior pituitary—which was confirmed by LEONARD, HISAW and FEVOLD (1932), WALLEN—LAWRENCE (1934), FEVOLD and HISAW (1934), EVANS, KORPI, SIMPSON, PENCHARZ and WONDER (1936), ASTWOOD (1941) and others—the way has been opened for a more detailed study of the inter-relations between the anterior pituitary and the ovaries. Of the two substances that FEVOLD et al. (1931) succeeded in isolating, one has proved

to regulate follicular development from the commencing antrum stage, and has, therefore, been designated the follicle-stimulating hormone (F. S. H.). The other substance has proved to regulate the luteinization, firstly of normal corpora lutea, and secondly of theca interna in the case of follicular atresia, and finally, also to regulate the estrogen incretion and ovulation. It has, therefore, been designated the luteinizing hormone (L. H.), (cf. FEVOLD, HISAW and LEONARD 1931, FEVOLD and HISAW 1934, WALLEN—LAWRENCE 1934, EVANS, KORPI, SIMPSON, PENCHARZ and WONDER 1936, FEVOLD 1939 a, b, 1941, FEVOLD and FISKE 1939, ASTWOOD 1941, and others). It has proved, however, that the incretion of F. S. H. and L. H. in the anterior pituitary is also affected by the estrogen incretion in the ovaries. When the estrogen incretion rises, the release of follicle-stimulating hormone is arrested, at the same time as the release of luteinizing hormone is promoted, (cf. SELYE, COLLIP and THOMSON 1935, WITSCHI and PFEIFFER 1935, WOLFE 1935, DEMPSEY 1937, FEVOLD 1939 b, FEVOLD and FISKE 1939, MERCKEL and NELSON 1940, and ASTWOOD 1941). Thus here we are in the presence of an intimate reciprocal action between the ovaries and the anterior pituitary. On the other hand, the relation between the anterior pituitary and the incretion of progesterone by the corpora lutea has long been a perplexing question. Hypophysectomizations have shown that during the earlier phase of pregnancy the hypophysis is necessary for the normal development and functioning of the corpora lutea. Further, in a series of investigations it has been shown that progesterone suppresses estrus and prevents ovulation. This implies, firstly that the anterior pituitary regulates the incretion of progesterone, and secondly that the incretion of progesterone affects the anterior pituitary. ASTWOOD and FEVOLD (1939) and BURDICK (1942) have shown, however, that if progesterone is supplied immediately after mating has taken place, the normal development of the corpora lutea is prevented. On the other hand, if progesterone is supplied after the corpora lutea have developed, the incretion activity of the corpora lutea is not impeded. From this ASTWOOD and FEVOLD concluded both that progesterone prevents the release of the gonadotropic substances (F. S. H. and L. H.) from the anterior pituitary, and that the progesterone incretion by the corpora lutea must be regulated by a third gonadotropic factor from the anterior pituitary. ASTWOOD (1941) also successfully isolated from the anterior lobe of the hypophysis of sheep a substance which was free from follicle-stimulating and luteinizing hormone. Further, ASTWOOD was able to prove that it was not identical with the growth and adrenotropic factors, and that it did not give rise to proliferation of the mammary lobules in hypophysectomized rats. This latter fact proves that in all probability it is not identical with prolactin, from which it otherwise proves difficult to separate it. This substance, which ASTWOOD calls luteotrophine, proved markedly to stimulate the incretion of progesterone, and it was therefore assumed to be the hypophysis factor

VOL.
28
194

which regulates progesterone incretion. In this connection it is of interest that EVANS, SIMPSON, LYONS and TURPEINEN (1941) found that deciduomata cannot be induced by means of traumatization in hypophysectomized female rats which have been treated with follicle-stimulating and luteinizing hormone from the anterior pituitary. On the other hand, if such females are treated with prolactin, deciduomata are obtained after traumatization, provided that ovariectomization has not been performed. Thus in this case the prolactin worked by way of the ovaries. SYDNOR (1945) also arrived at similar results. Viewed in the light of ASTWOOD's results, this indicates that the prolactin employed in these experiments was not free from luteotrophine. ASTWOOD has also especially pointed out the difficulties in separating these substances from each other. These experiments with prolactin therefore constitute a certain support for the correctness of the results reached by ASTWOOD (1941).

If we proceed from the assumption that the anterior pituitary of the female secretes three different gonadotropic substances, the hormonal regulation of reproduction may conceivably take place as follows (cf. also ASTWOOD 1941). Oogenesis and follicular development up to the commencing antrum stage take place independently of the anterior pituitary. Under the influence of external factors the anterior pituitary enters an active incretion phase, follicle-stimulating hormone being increted and released. As a result of this, vesicular follicles are formed and continue to grow. A spontaneous estrogen incretion appears to accompany this follicular growth and stimulates the anterior pituitary to increte luteinizing hormone. As a result, the granulosa in the larger follicles proliferates, ovulation takes place, and the corpora lutea are formed. At the same time the luteinizing hormone appears to stimulate estrogen incretion, resulting in the release of follicle-stimulating hormone from the anterior pituitary being suppressed, which in its turn implies that, after the commencing antrum stage, follicular development ceases. By the release of luteotrophine from the anterior pituitary the corpora lutea are stimulated to increte progesterone. This leads, firstly, to the release of luteinizing hormone from the anterior pituitary being suppressed, which in its turn leads to a decreasing estrogen incretion and the cessation of estrus, and secondly, to the uterine mucosa being prepared for implantation. Progesterone incretion, however, is not completely dependent in all animals on the anterior pituitary, but towards the end of pregnancy this regulation may be taken over by substances, the so-called cyonins (ASTWOOD and GREEP 1939), which are increted by the placenta. The hormonal mechanism sketched here applies only to the cases where ovulation and the formation of corpus luteum are not dependent on mating. In the case of the non-spontaneous ovulation, copulation will probably condition the release of luteinizing hormone, and in the case of the activity in the corpora lutea in mice and rats which is dependent on mating, copulation will probably condition the release of luteotrophine.

Since our knowledge of the endocrine interplay between the anterior pituitary and the ovaries still is not wholly elucidated, the above attempt to explain the endocrine regulation of reproduction can by no means be looked upon as definitive. It can, however, serve as a working hypothesis, on which to base an attempt to analyse the causes of the delayed implantation.

As has been pointed out earlier, the delayed implantation in mink appears to be due either to a continuation of estrogen incretion after ovulation, and at the same time an absence of progesterone incretion, or to the estrogen suppressing the effect of the progesterone. The latter possibility does not seem likely, however, in view of the inactive picture exhibited by the corpora lutea during the free vesicle stage. The complete or partial absence of progesterone incretion during the free vesicle stage appears, in its turn, to be due to a shift in the balance between the incretion of gonadotropic substances from the anterior pituitary or to the complete absence of the incretion of some substance from it. The normal follicular development, ovulation, and formation of the corpora lutea, indicate that the incretion of both F. S. H. and L. H. is not disturbed. On the other hand, the inactive appearance of the corpora lutea and the absence of the progesterone effect in the uterus indicate that the factor which regulates progesterone incretion is not secreted. The results of ASTWOOD, EVANS et al. and SYDNOR indicate that this factor is luteotrophine.

The question then presents itself, what may be the causes of the great variation in the interval between ovulation and the release of luteotrophine from the anterior pituitary in the case of mink. The circumstance that this interval is longer at the beginning of the mating season than towards the end of it, indicates that, at the beginning of the mating season, the anterior pituitary is not ready for the incretion of this substance. In such cases copulation effects the release of L. H., so that ovulation takes place, and the corpora lutea are formed, but as luteotrophine is not increted, the latter remain in an inactive stage.—An interesting parallel is provided by the conditions in mice, where in certain cases copulation does not elicit the normal corpus luteum function, with the result that the blastula cannot be implanted (cf. BALL 1940).—Consequently the estrous state continues until the anterior pituitary begins to increte luteotrophine. This activates the incretion of progesterone by the corpora lutea, so that the release of L. H. ceases, the incretion of estrogen decreases, the uterine mucosa is prepared for implantation, and the embryonic development proceeds normally.

The results obtained from the studies of delayed implantation in mink thus constitute a further strong argument in favour of there being three different gonadotropic factors in the anterior pituitary. By this the present work may be said to have come into contact with one of the most far-reaching problem involved in mammalian reproduction.

VOL.
28
194

VIII. FACTORS AFFECTING FERTILITY.

Fertility is the net result of all the phases of reproduction, from copulation to parturition. As HAMMOND (1941) pointed out, it is determined, firstly by the number of ovulated eggs, secondly by how many of them are fertilized, and thirdly by how many of the fertilized eggs are implanted and develop normally up to parturition. To obtain a picture of the effectivity of reproduction in mink and the factors which affect it, the experimental and the statistical data have been analysed.

A. THE CORRELATION BETWEEN THE NUMBER OF OVULATED AND IMPLANTED EGGS AND THE NUMBER OF CUBS BORN.

MAINLAND (1927) found that 0.1—1.5 per cent of all the follicles in ferrets were pluriovular. In the case of mink only one such follicle was met with among the thousands of ovarian sections which were scrutinized. One can therefore assume that in mink the number of ruptured follicles constitutes a very safe measure of the number of ovulated eggs. In what follows, therefore, when mention is made of the number of follicles ruptured, or of corpora lutea formed, this may be taken as equivalent to the number of ovulated eggs.

Table 35. *Number of ruptured follicles.*

	Number of ruptured follicles														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Number of ovulations . . .	2	5	6	14	24	16	14	5	9	8	5	5	4	2	1

The number of corpora lutea formed after the first mating in the case of 120 ovulations from the experiments are collocated in table 35. As is seen, the number of corpora lutea varies from 3 to 17, and on an average 8.73 ± 0.30 were formed. In table 36 this material has been arranged according to the dates of matings, from which it emerges that there is a tendency towards a greater

Table 36. *Influence of date of mating on number of ovulated follicles.*

	Date of matings in March			
	3—6	7—14	15—22	23—
Number of ovulations	16	29	51	24
Total number of ovulated follicles	131	260	471	192
Mean „ „ „ „	8.19	8.97	9.24	8.00

number of ruptured follicles in the middle than at the beginning and the end of the mating season.

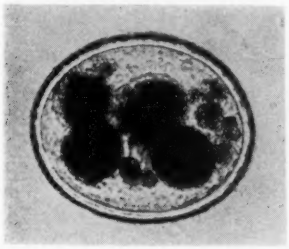
Owing to the way in which the experiments were carried out, it is not possible to determine how large a proportion of the ovulated eggs were fertilized. On the other hand, the number of implanted foetuses was computed for 21 females which were killed during the first stage of pregnancy, the numbers in the right and left uterine horns being entered separately. For the right uterine horn this was 4.05 and for the left 3.24. The difference and its mean error, 0.81 ± 0.32, indicate a significant difference between the two uterine horns in respect of the number of implantations. It has not been possible to determine whether this is due to a difference in the two ovaries in respect of the number of ovulated eggs or to other factors, as when the ovaries were fixed they were not kept distinct. Altogether for these 21 females an average of 7.29 ± 0.29 foetuses had been implanted. As it appears probable that a number of implanted foetuses had succumbed and been resorbed before the autopsies, this value is probably lower than the actual value for the number of implanted blastulae. The fact that a considerable number of ovulated eggs succumb before implantation is proved also by the circumstance that such eggs are often met with in the uterus. In fig. 73—74 examples of such eggs are shown.

To render possible a comparison between the above values for the number of ovulated eggs and implanted foetuses and the number of cubs born, the last-mentioned value has been calculated for the total Quebec material. The average litter size for 2,380 births was 4.37 ± 0.005. If this value is compared with the number of implanted foetuses, it is found that a very large proportion of them succumb before parturition. It was possible to verify this, too, from the experiments. In this connection may be mentioned the remarkable circumstance that, in the majority of cases, the foetal resorption affected the foetuses which were implanted nearest the corpus uteri. Examples of foetuses in process of being resorbed are shown in fig. 75.

If the number of ovulated eggs is compared with the number of implanted foetuses and cubs born, it is found that of 100 eggs an average of 83.7 are implanted, and 50.2 result in cubs. Thus the greater number succumb after they have been implanted. These figures refer, however, only to females which ovulated, had implanted foetuses, and gave birth to cubs respectively. The fertility in a total material is naturally lower than this owing to the absence of ovulation, fertilization and implantation, or to the total resorption of foetuses in a number of females. The frequency of such females varies greatly, however, depending on the system of mating employed. In the above-mentioned Quebec material the number of such females was 20.2 % of the total.

It appears from the results obtained above that the intrauterine foetal mortality in mink is great. This is also the case, however, among other mul-

VOL
28
194



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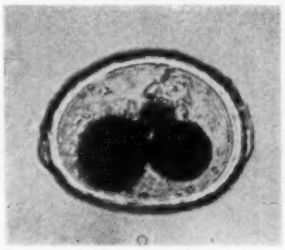

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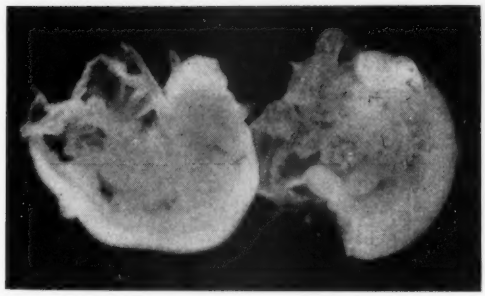

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Figs. 73—75. — 73—74. Dead eggs. (180 ×.) — 75. Foetuses undergoing uterine resorption. (6 ×.)

tiparous animals, such as ferrets, rabbits and pigs, cf. ROBINSON (1921), MARSHALL and HAMMOND (1933), HAMMOND (1941), BRAMBELL (1942) and BRAMBELL and MILLS (1944).

B. BREED, AGE, DATE OF MATING, LENGTH OF GESTATION AND GENETIC FACTORS.

Owing to the great influence the mating system employed has on fertility and the differences prevailing in this respect between the Quebec and Alaska materials, as described in section III, the comparisons between the breeds have been based on the once-mated females. In fig. 76 are shown the variation between the two breeds in respect of the size of litters. On an average the Quebec females gave birth to 4.266 ± 0.066 and the Alaska females to 5.173 ± 0.088 cubs. The animals of the Alaska breed thus exhibit a considerably greater fertility, which is probably due to their larger size.

Investigations by JOHANSSON (1928, 1938, 1945) and JOHANSSON and HANSSON (1943) have shown that in pigs, sheep, silver foxes and blue foxes there is relation between the age and fertility of the females. In mink this

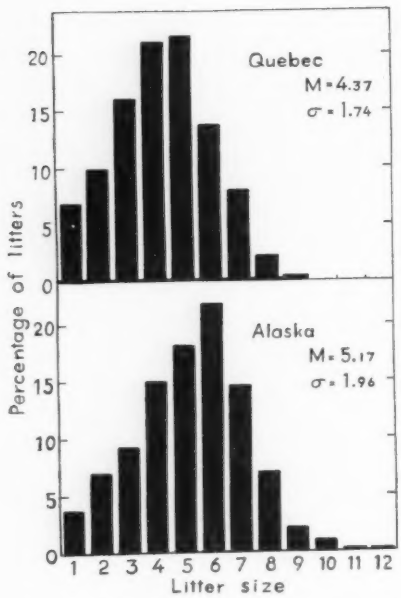

Fig. 76. Variation in sizes of litters in Quebec and Alaska females.

relation has been studied on the basis of the total Quebec material (table 37 and fig. 77). The corresponding quadratic regression line, based on the averages of each age, has the equation $y = 4.25 + 0.357x - 0{,}0973x^2$, where y is the size of the litters and x the age in years of the females. Table 37 and fig. 77 show that the fertility rises from the first to the second year and subsequently progressively decreases. It is to be noted, however, that the relation will probably have been affected by selection, for in practical breeding a female is eliminated if she gives birth to a small number of cubs. The older females therefore exhibit a progressively better average fertility. If this selection had not asserted itself, the fertility would probably have decreased more than is actually indicated.

JOHANSSON and HANSSON (1943) found that the number of lambs born per ewe was greater in the middle than at the beginning and the end of the parturition season. To ascertain whether the same thing is true also of mink, the once-mated Quebec and Alaska materials are brought together in table 38. As appears from this table, there is a tendency towards a larger number of cubs after mating in the middle of the mating season than after mating at the beginning or the end.

It has previously been shown that there is a negative correlation between the number of cubs born and the length of the gestation period (see p. 24). To illustrate this correlation further, in table 39 the above-mentioned Quebec and Alaska females have been grouped up according to the length of the gestation period, and the average number of cubs born has been calculated. The tendency towards a decline in fertility in the case of prolonged gestation

Table 37. *Influence of age of the female on size of litter.*

	Age of the females in years					
	1	2	3	4	5	6
Number of litters	1,298	681	322	120	26	11
Mean size of litter	4.43	4.69	4.50	4.12	3.42	3.00

which the table shows, will probably be connected with an increased mortality during the free vesicle stage.

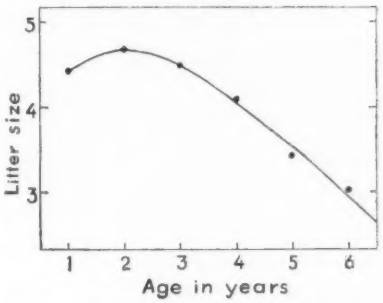

Fig. 77. Size of the litter in relation to the age of the female.

It has been shown in a large number of investigations with different kinds of animals that fertility is affected by genetic factors, and the difference in fertility between Quebec and Alaska mink is in all probability due to such factors. To investigate whether there are any differences within the breeds which can be ascribed to heredity, an analysis of variance has been made of the size of litters for 171 Quebec females which gave birth to cubs 3 years in succession. The results of this analysis have been collocated in table 40, from which it appears that there is a tendency towards a greater variation between

Table 38. *Influence of date of mating on size of litter.*

	Date of mating in March				
	—6	7—12	13—18	19 - 24	25—
Quebec:					
Number of litters	81	285	262	54	15
Mean size of litter	4.19	4.30	4.21	4.50	4.33
Alaska:					
Number of litters	4	31	206	184	69
Mean size of litter	4.75	4.93	5.38	5.15	4.77

females than within females. The intra-class correlation calculated with the guidance of the variances was 0.118, which implies that 11.8 % of the total variation in the fertility is due to individual differences between females, which must probably be largely ascribed to hereditary differences. Thus there is a

Table 39. *Influence of length of gestation on size of litter.*

	Length of gestation in days						
	—44	45—48	49—52	53—56	57—60	61—64	65—
Quebec:							
Number of gestations	51	191	191	152	66	32	14
Mean size of litter	4.67	4.45	4.38	3.91	4.32	3.84	3.50
Alaska:							
Number of gestations	86	141	171	77	12	7	—
Mean size of litter	5.06	5.53	5.11	4.84	5.17	4.71	—

Table 40. *Analysis of variance of size of litter for 171 females each with three consecutive litters.*

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Ratio of mean squares
Between females	170	489.61	2.880	$\frac{2.880}{2.200} = 1.309^*$
Within „	342	752.36	2.200	
Total	512	1,241.97	2.426	

certain, though slight, possibility of improving the fertility in mink by means of selection.

C. SYSTEM OF MATING.

As was shown in section V, the riding of a female without copulation may elicit ovulation. These ovulations are very serious phenomena, partly owing to their frequency, and partly because they often lead to a supression of pregnancy. Therefore, in practical breeding, males which show a tendency to ride the females without mating should immediately be eliminated, even though this cannot entirely prevent such ridings. It is therefore of great importance that the females should be mated at the latest 2 days after such a riding, in order to ensure the fertilization of the eggs.

In order to study if the system of mating affects the number of pregnant females and the number of cubs born, a material comprising 2,233 pregnancies was selected. The females were mated one, two or three times. In the last case with at least 7 days between the first and the second mating. As appears from table 41 the mean litter size for the once-mated females was 4.11 and the average number of cubs per female 2.77. 32.6 per cent of the once-mated females did not give birth to cubs. The females which were re-mated at intervals of 1 and 2 days had a mean litter size of 4.21 and 4.54 and the average number of cubs per female was 3.83 and 3.73. This increasing fertility is also reflected in the per cent of females which did not give birth to cubs. This improvement in fertility appears to be mainly due to two causes. As was shown in section V, the female mink ovulates 36—37 hours after mating. If it is assumed that the unfertilized egg has the same duration of life as in the case of the ferret, (cf. HAMMOND and WALTON 1934 a), then in the majority of cases they could still be fertilized 54—60 hours after a mating. That means that re-mating 1 to 2 days after the first mating can result in fertilization of the eggs which were ovulated after the first mating. The increase in mean litter size and the reduced number of barren females indicates that this is actually the case. A contributory cause of the decrease in the number of barren females

Table 41. *Influence of system of mating on fertility in 2,223 Quebec females. The females which were mated three times, had at least a 7-days interval between the first and the second mating.*

Litter size	Number of females with following number of matings:														
	One mating	Two matings. Interval between matings in days									Three matings. Interval between 2nd and 3rd mating in days				
		1	2	3-4	5 6	7-8	9-10	11-12	13-	7-	1	2	3-4	5-6	7-
0	227	9	50	11	13	29	28	16	12	85	4	33	7	4	6
1	40	4	11	3	—	5	6	3	2	16	—	12	2	—	—
2	50	12	22	7	5	17	16	6	12	51	2	27	6	1	1
3	86	16	26	5	4	16	27	6	14	63	11	37	4	1	4
4	100	14	50	12	7	34	27	20	19	100	12	69	3	3	8
5	85	28	53	7	4	29	40	24	20	113	14	82	7	4	11
6	63	7	34	7	1	17	27	27	14	85	9	56	13	1	6
7	34	7	23	1	1	8	10	5	8	31	5	16	4	1	5
8	9	2	8	—	—	1	2	4	5	12	2	4	2	—	—
9	2	—	1	—	—	1	1	—	1	3	—	3	—	—	—
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Total number of females	696	99	278	53	35	157	184	111	107	559	59	339	48	15	42
Number of cubs per female	2.77	3.83	3.73	3.09	2.37	3.46	3.72	4.16	4.05	3.80	4.41	4.04	4.06	3.33	4.36
Percentage of unfertile females	32.6	9.1	18.0	20.8	37.1	18 5	15.2	14.4	11.2	15.2	6 8	9.7	14.6	26.7	14.3
Mean litter size	4.11	4.21	4.54	3.90	3.77	4.24	4.38	4.86	4.56	4.48	4.73	4.48	4.76	4.55	5.08

will probably be that, if, for some reason, the first mating did not elicit ovulation (cf. section V) the second mating may do so.

When the females were re-mated at intervals of 3—4 days, the mean litter size is considerably lower than for the females which were re-mated at an interval of 1 to 2 days. The number of females which did not give birth to cubs has also increased. In comparison with the once-mated females, however, the average number of cubs per female is somewhat higher, owing to a decline in the number of barren females. The cause of this change will be that the females which did not ovulate after the first mating did so after re-mating. The decline in fertility as against that of the females which were re-mated at an interval of 1 to 2 days is in all probability entirely due to the fact that re-mating can no longer fertilize eggs which were ovulated after the first mating.

The females which were re-mated at a 5—6 days interval exhibited very low fertility, as appears from table 41. Thus the mean litter size is only 3.77, and the average number of cubs per females 2.37. This last low value is chiefly

due to the fact that the number of barren females was very high, i.e. 37.1 per cent. Except in one respect, this category of females is comparable with the females which were re-mated at a 3—4 days interval. The difference is that in the case of re-mating 3—4 days after a mating no fresh ovulation takes place, as it often does when the females are re-mated at a 5—6 days interval (see section V). At that stage only a small number of follicles had reached such a stage of development that they could be made to ovulate and therefore such ovulations mean decreased fertility.

When the females are re-mated at longer intervals than 6 days, the fertility rises steeply, at the same time as the number of barren females declines. This change continues, as appears from the table, up to the 11—12 days interval. This continuous increase indicates that increasing numbers of follicles have had time to develop up to the stage where they can be made to ovulate. With longer intervals than 12 days between the first and second matings the fertility shows a tendency to fall.

If a comparison is made between the females re-mated at a longer interval than 7 days after the first mating and the females re-mated at varying intervals after the second mating, the same systematic change in fertility is found as when the once-mated females are compared with the twice-mated ones. Re-mating 1—2 days after the second mating thus results in an increase in fertility. On the other hand, with re-mating after 5—6 days the fertility declines, but rises again with longer intervals between the matings (see table 41). This series thus verifies the preceding series.

If a comparison is made between once-mated females and females which were re-mated once and twice at intervals of at least 7 days, a clear improvement in fertility is met with. The mean litter size rises from 4.11 to 4.48 and 5.08 respectively, and the average number of cubs per female from 2.77 to 3.80 and 4.36 respectively. The number of barren females decreases from 32.6 to 15.2 and 14.3 respectively. The last mating for the latter females gave rise to fresh ovulation, and thus, from the point of view of mating, the difference between the females is that the two last-mentioned categories had been mated once or twice previously. That the females which were mated twice and three times exhibit such considerably improved fertility will probably be the result of several co-operating causes. In the first place the females which permitted several matings are probably more active from the sexual point of view and at the same time more fertile. In the second, it has been shown in section V that, if a female is mated later in the estrus, implantation takes place earlier than if she is mated at the beginning of estrus. Further, in section III it was shown that females which were mated late in the mating season had a shorter gestation period than females mated early. The re-mated females were quite naturally mated late both in respect of the beginning of the estrus and of the mating season. As there is a negative correlation between the length of the

VOL.
28
194

Table 42. *Analysis of variance of fertility in re-mated Quebec females.*

Source of females and variation	Degrees of freedom	Sum of squares	Mean squares	Ratios of mean squares
All females:				
Between mating intervals.				$\frac{12.50}{4.95} = 2.53$
Linear regression	1	12.50	12.50	$\frac{19.46}{4.95} = 3.93^{**}$
Deviation from linear regression .	6	116.77	19.46	
Within mating intervals (error) . .	1,017	5,031.67	4.05	
Total	1,023	5,160.91	5.04	
Only females with litters:				
Between mating intervals.				$\frac{11.68}{2.79} = 4.19^{*}$
Linear regression	1	11.68	11.68	
Deviation from linear regression .	6	40.45	6.74	$\frac{6.74}{2.79} = 2.42^{*}$
Within mating intervals (error) . .	848	2,364.47	2.79	
Total	855	2,416.60	2.83	

gestation period and fertility, the re-mated females should in consequence exhibit greater fertility than the once-mated.

For the sake of investigating whether the changes in fertility are significant, an analysis of variance has been made, firstly of the mean litter size and secondly of the average number of cubs per female. As, quite naturally the differences between the once-mated and the re-mated females are significant, and as it was not considered desirable to mix together different categories of females, this analysis only embraces the twice-mated females. To endeavour to eliminate approximately the effect which mating at different intervals after the onset of estrus, and at different times during the mating season, has on the length of the gestation period and therewith on fertility, the variance between mating intervals (see table 42) has been divided up into deviations due to the linear regression and deviations from the regression line. The latter variation would then correspond to the influence of the mating system itself on the fertility. As appears from the table, there is a tendency towards a verified regression in the material. If the deviations from the regression line is compared with the error, a very definite significance is found in the average number of cubs per female, and a little lower significance in the mean litter size. Thus this proves that the mating system has a pronounced influence on fertility. If all the females, thus even those which were mated once and three times, had been included in the analysis, this tendency would have been still more pronounced.

D. CONCLUSIONS.

The experimental investigations and the statistical analysis have shown that the reproduction of mink is affected by a number of factors which assert themselves in respect of fertility. Like other multiparous animals, the mink has a high intra-uterine foetal mortality, especially in the later stage of pregnancy. Owing to ovulation conditions, and perhaps above all to the occurrence of delayed implantation, the fertility is very dependent on the mating system employed. On the basis of the experimental investigations carried out and the statistical analyses made, certain general rules can be established for the mating of mink. Thus mating with males which show a tendency to ride females without mating should be avoided. If such riding has taken place, the female should be mated with another male at the latest 2 days afterwards. When a female has been mated for the first time during the season, re-mating should be tried on the first and second days after this mating. On the other hand, a female must never be re-mated 3—6 days after the first mating. From the 7th day after the first mating the female can be mated again, and then, too, re-mating should be tried on the first and second days after that second mating. After at least a further 7 days the female can be tried again, according to the same rules.

Apart from the fact that this system of mating simplifies the work of breeding, during the last two years it has proved to lead to greater fertility in practical breeding.

VOL
28
194

SUMMARY.

The present work, entitled "The physiology of reproduction in mink, Mustela vison, SCHREB., with special reference to delayed implantion", is based on investigations carried out during the years 1939—46.

The results of the statistical and experimental investigations may be summarized under the following points, which correspond to the different sections in the present work:

I. II. After an introductory survey of earlier studies of reproduction within the genus Mustela, a description is given of the writer's material and of the general working methods.

III. The mating season falls during March and the beginning of April and the littering season during the end of April and the beginning of May. The dates are influenced by the breed and age of the female and by the outdoor temperature.

The length of copulation increases as the mating season advances. The

intervals between two consecutive matings tend to centre round the two values 1—2 and 7—10 days.

The mean length of gestation for 697 Quebec and for 494 Alaska females was 51.33 and 49.01 days respectively, the coefficient of variation being 4—6 times as great as for other farm animals. The length of gestation is greatly influenced by the date of mating. The relation yields the function $y = 62.0 - 1.0846x + 0.01804x^2$, where y is the length of gestation and x the mating date in March.

IV. Owing to the shortness of ligamentum ovarii proprium the ovary is fixed in the immediate neighbourhood of the distal end of the cornua uteri. Owing to the position of the ovary and the shape of the mesovarium and the mesotubarium, a practically completely closed bursa ovarii is formed.

The ovaries are generally bean-shaped. Under the germinal epithelium there is a well developed tunica albuginea, from which connective tissue lamellae run into the cortex and divide it up into irregular columns and nests. The interstitial glandular tissue is strongly developed in the cortex. The medulla is confined to the parts around the hilus of the ovary.

The tuba runs round the ventral surface of the bursa ovarii and during its course forms 10—11 regular coils. The infundibulum is weakly developed, which has been considered to be a result of the well-developed bursa ovarii.

The long tapering uterine horns fuse immediately in front of the cervix and form a weakly developed corpus.

Placentation leads to the formation of a placenta zonodiscoidalis, in the antimesometrial centrum of which are formed specific hematomae. These hematomae seem to serve to supply the foetuses with hemoglobin.

V. Nine different stages can be distinguished in the growth of the follicles. In fixed material the follicle which is ready for ovulation attains an average diameter of 1,000—1,100 μ, as against 100 μ for the egg. Already when the average diameter of the follicle is 500 μ, the growth of the egg has practically ceased.

Females which have not been mated or allowed to play with males do not ovulate, but their follicles form so-called cystic follicles. After copulation the follicles grow rapidly, and ovulation follows after 36—37 hours. Riding by males without copulation also generally elicits ovulation.

When a female is re-mated at an interval of less than 5 days, the second mating does not elicit another ovulation. If the interval is 5—6 days the second mating sometimes does give rise to fresh ovulation. If the intervals between the matings are longer than 6 days, the second mating always elicits fresh ovulation.

When the female ovulates again, the fertilized egg from the previous ovulation generally succumbs. In one case, however, a blastula from the first ovulation was found in the uterus at the same time as fertilized two-celled eggs

were found in the tuba from the second ovulation. This indicates that superfetation may occur.

An analysis of variance of the number of ruptured follicles in the two ovaries at two successive ovulations showed a tendency in the ovaries together to ovulate a certain fixed total of follicles in each ovulation. This shows that the number of ovulated follicles is determined by factors whose effects are not restricted to the individual ovary. It is assumed that this factor is estrogen, which works by regulating the release of the follicle-stimulating factor (F. S. H.).

VI. By mating females once and carrying out autopsies at varying intervals from the mating, it has been found that, after its passage through the tuba, the fertilized egg enters a stage of relative rest, varying in length. That causes the great variation in the length of the gestation period.

VII. The length of gestation decreases with increasing temperature during the mating season.

Irradiation of females during the late anestrus stage hastens the transition to pro-estrus and leads to significative proliferation in the ovaries and uterus. Irradiation of females before and after mating reduces the length of gestation.

The changes in the ovaries, tuba, uterus, and vagina during the sexual cycle have been studied with the object of discovering whether there are disparities correlated with the delayed implantation.

In the development of the corpora lutea 4—5 different stages were distinguished. After a stage of normal granular and vascular proliferation, the corpora lutea generally enter into an inactive phase, which corresponds to the stage of relative rest in the embryonic development. The cyclic changes in the evolution and involution of the follicles and corpora lutea greatly influence the size of the ovaries. During pregnancy the ovaries are 1.7—1.9 times as large as during anestrus.

The tuba of the female mink exhibits cyclic changes similar to those shown by other animals. There is a striking divergence, however, in that after ovulation the tuba again resumes its estrus character, without passing through a typically degenerative stage. If the female is not re-mated, this estrus stage persists until immediately before implantation.

The changes in the uterus during pro-estrus and estrus are of a normal character. During the time the blastula lies free in the uterus, however, no progesterone influence can be traced. In connection with implantation progestational proliferation appears, as a result of the renewed activity of the corpora lutea.

Studies of the vaginal secretion have shown that anestrus passes over to pro-estrus as early as in January, pro-estrus then passing by degrees into estrus. After ovulation a partial desquamation of the cornified layer takes place, but this does not proceed so far that the vaginal lumen is invaded by leukocytes.

VOL
28
194

Immediately after this stage, the vaginal secretion re-assumes the estrus character. If the female is not re-mated, this stage persists until suddenly a final desquamation of the cornified layer occurs, followed by a massive infiltration and invasion of mainly polymorphonuclear leukocytes. The interval between mating and the final desquamation and the length of the gestation period exhibits a correlation of $r = 0.918^{***}$, and the value of the regression is $b = 1.079$.

Attempts were also made to influence implantation by administering different gonadotropic hormones.

The administration of varying amounts of synthetic progesterone, with and without simultaneous supplies of small amounts of estrogen, did not affect the estrus condition or implantation in normal, mated females. As strong reasons argue in favour of this negative result being due to the fact that the ovaries secrete estrogen, which suppresses the effect of the progesterone, ovariectomy was performed on mated females, after which progesterone was administered. As a result of the ectomization, the estrus condition ceased, and the administration of progesterone led to progestational proliferation.

The administration of estrogen in association with mating did not change the female's estrus condition or the time of implantation. A fall in the number of cubs born was considered to be due to the supplies of estrogen having supressed follicular development.

The administration of gonadotropic substances from blood (P. M. S.) and from pregnancy urine (P. U.) led to an increased intra-uterine foetus mortality and to increased length of gestation.

In a discussion of the causes of the delayed implantation, it is advanced that it cannot be due to a cessation of growth in the blastula, but that it must be due to the uterine mucosa not being prepared for placentation. This in its turn appears to be due to a shift in the balance between estrogen and progesterone, which in its turn must be the result of a change in the balance between the endocrine factors in the anterior pituitary which regulate the activities of the ovaries. Investigations by Astwood (1941) indicate that, in addition to a follicle-stimulating factor (F. S. H.) and a luteinizing factor (L. H.), the anterior pituitary also secretes a substance (luteotrophine) which regulates progesterone incretion. If this observation is correct, the delayed implantation would appear to be due to a delayed release of luteotrophine from the anterior pituitary.

VIII. Investigations as to fertility have shown that of 100 ovulated eggs an average of 83.7 are implanted and that about 50.2 of them result in cubs. This applies to females which ovulated, had implanted foetuses and produced litters. The number of females in the same material which did not produce cubs was 20.2 per cent.

Fertility is affected by the breed, age, time of mating, and length of gesta-

tion of the females. 11.8 per cent of the total variation in fertility may be ascribed to individual differences between females.

The system of mating has a marked influence on fertility, and therefore, with the guidance of the experimental investigations and the statistical analysis, rules have been proposed for the mating of the female.

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VOL
28
194

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VOL
28
194

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VOL
28
194

HYDROPHILOUS AND XEROPHILOUS LABYRINTHODONTS

BY

A. P. BYSTROW

(With 13 figs.)

VOL. 28 1947

INTRODUCTION.

In 1938 a paper was published in the Russian Zoological Magazine by MEDVEDEV about cutaneous vessels of modern amphibians. By means of preparation the author has stated some very interesting facts. In particular it has been shown that the distribution of branches of the arteries supplying blood to the skin (art. cutanea) as well as the situation of the vein branches (vena cutanea magna) of different representatives of Anura depends on their mode of life. Those who spend on land the greater part of their life, or who—as adults—do not live in water at all, have the main branches of blood vessels situated on the lateral faces of their body. This distribution of the vessels is due to the fact, that the air surrounding the animal, makes the cutaneous respiration possible in all the points of the body. MEDVEDEV's observations have shown that, for instance, the Rana temporaria which spends most of its life on the shores of rivers and lakes, and not in water, as well as toads which are known to be typical terrestrial members of Anura and, as adults, never live in water, have such a ramification of cutaneous arteries and veins (fig. 1 A).

It has been shown that the Anura which during the whole of their life hardly ever leave fresh-water basins, have quite a different distribution of cutaneous vessels. These have the branches of the cutaneous arteries and veins situated on the dorsal side of the body, which in amphibian staying in water is exposed to the action of air (fig. 1 B).

Such a situation of the vessels is due to the fact, that the oxygen contents of the air is 30 times greater than that of the water, and for this reason the cutaneous respiration is particularly intensive on the spot of direct contact with air and not with water.

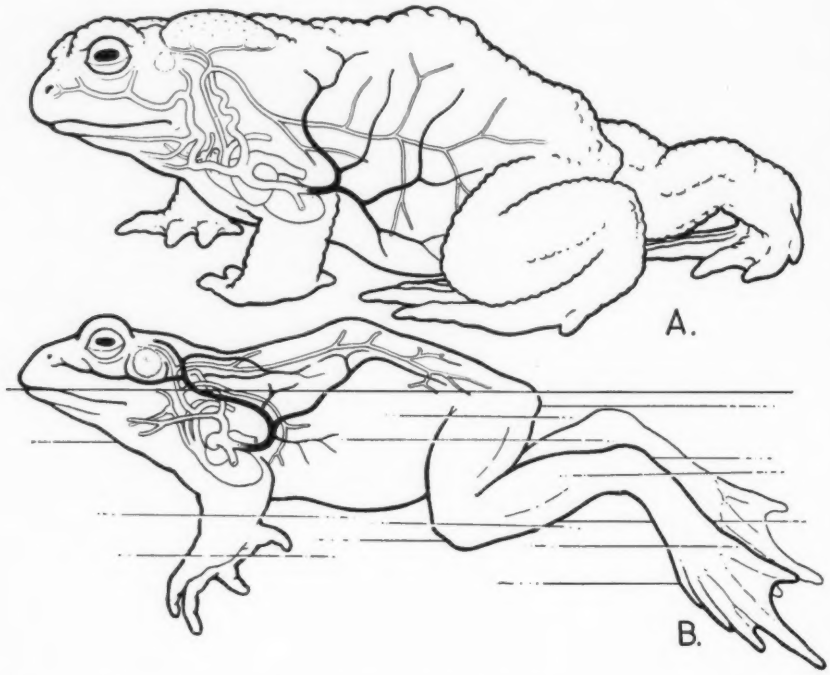

Fig. 1. *A.* Cutaneous vessels in toad (Bufo bufo); *B.* Cutaneous vessels in frog (Rana ridibunda).

VOL
28
194

MEDVEDEV has observed that such typical aquatic forms of Anura, as the Bombina bombina and Rana ridibunda have the principal cutaneous vessels ramified mostly on the dorsal side of the body.

All these interesting observations have shown the cutaneous respiration in modern amphibians to be a very important addition to the gaseous exchange through the lungs.

This is very well proved by the so-called "hairy frog"—Astylosternus robustus (fig. 2). During the breeding season the males of the species have numerous vascular villosites having a likeness to hair, developed on the lateral faces of their body and on their hind limbs. By means of these formations the "hairy frog" has an intensive cutaneous respiration, which compensates for the defective function of the greatly reduced lungs.

It is necessary to add that in cases where the lungs of the modern amphibian prove to be not enough developed or to be fully lacking, the cutaneous respiration is the principal or the only means of gaseous exchange. Such a representative of the Urodela, as Cryptobranchus alleganiensis has the capillaries penetrating the epidermis to a position very near the surface (NOBLE 1931).

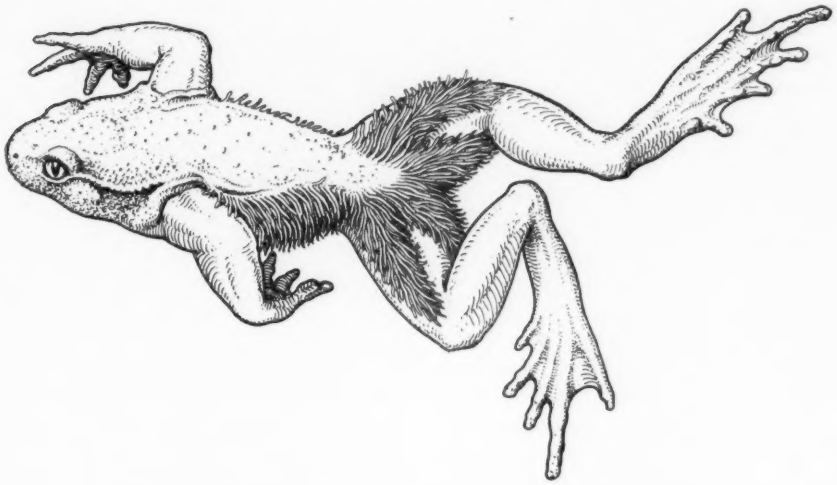

Fig. 2. "Hairy frog"—Astylosternus robustus. After Noble.

In lungless salamanders (in the Plethodontidae) the gaseous exchange is realized only through the skin and epithelium of the mouth and pharynx.

We are sorry to say we have no information whatever on the structure of lungs of the fossil amphibians. It is probable, however, that the Carboniferous, Permian and Triassic stegocephalians hardly differed of the modern Urodela. Anyway the construction of their lungs is supposed not to be more complicated than that of the existing amphibians.

Therefore we may with reason suppose the cutaneous respiration in stegocephalians to play in some cases a considerable rôle in the gaseous exchange; possibly in some forms it is more intensive than the gaseous exchange through the lungs.

Without a doubt the conditions of life of the labyrinthodonts from the Devonian up to the Triassic have been sufficiently various. In some cases the archaic amphibians had to adapt themselves to living in areas with relatively arid climate and with insufficient fresh-water basins, in other cases—to existing in regions with humid climate and numerous rivers and lakes.

All these facts had to influence in some way or other the structure and functions of some of their organs, in particular of those which are connected with the gaseous exchange.

All our ideas of the fossil amphibians are known to be formed on the base of studying their skeletons only; we are sorry to state the impossibility to study those systems of organs of which nothing is left soon after the death of the animal.

Therefore we must not omit a single detail of the skeleton structure which

makes it possible to understand—if only in general outline—the functions of those symptoms of organs which prove to be inaccessible for direct investigation.

The study of the dermal bones structure of various stegocephalians of the Permian and Triassic resulted in my assembling information which seems to allow me to suppose some forms of labyrinthodonts to have a very intensive cutaneous respiration, whereas in other forms it is but very insignificant and even fully absent. In addition to this I suppose, that having in view some other peculiarities of the skeleton structure, the labyrinthodonts having an intensive gaseous exchange through the skin may be considered as hydrophilous forms and those deprived of cutaneous respiration—as xerophilous forms.

According to the finds of Permian and Triassic deposits of the USSR which I have at my disposal, labyrinthodonts of both these types were not rare in the end of paleozoic and in the beginning of the mesozoic. But I am very sorry to say that in my material some of them were represented only by small fragments of the skull or by broken pieces of dermal bones. Of course, it could not allow me to form quite a clear idea of their general appearance. Therefore, having in view the description of hydrophilous and xerophylous labyrinthodonts, I have used only well preserved and minutely investigated forms.

All the numerous transparent sections of dermal bones, as well as all the illustrations have been made personally by myself.

VOL. 28 194

THE HYDROPHILOUS LABYRINTHODONTS.

A good example of a hydrophilous labyrinthodont may be found in the neorhachitomous stegocephalian Benthosuchus sushkini. This form has been found for the first time in 1927 in the eotriassic deposits on the Sharjenga-river (Efremov 1929). The excavations resulted in giving several full, well preserved nondeformed skulls, a large number of skeleton bones and numerous fragments of dermal bones. All these parts of the skeletons had belonged to animals of different individual age (Bystrow and Efremov 1940). The skull of the Benthosuchus was wedge-shaped; its length varied between 140 and 229 mm. These skulls appear to have belonged to middle-aged specimens, for, according to separate fragments of dermal bones, the skull dimensions of old Benthosuchus attained probably about 700 mm of length. The skull length of the youngest of the known labyrinthodonts of this species was only 27.5 mm.

The exterior face of the dermal bones of the skull and lower jaw of the Benthosuchus are covered by a round-celled sculpture which is typical for labyrinthodonts. On the skull and on the lower jaw furrows are to be clearly seen, which are marks of canals of a seismosensory system, which had passed here (fig. 3). The presence of these furrows allows to affirm with safety that the canals themselves of this labyrinthodont had been well developed.

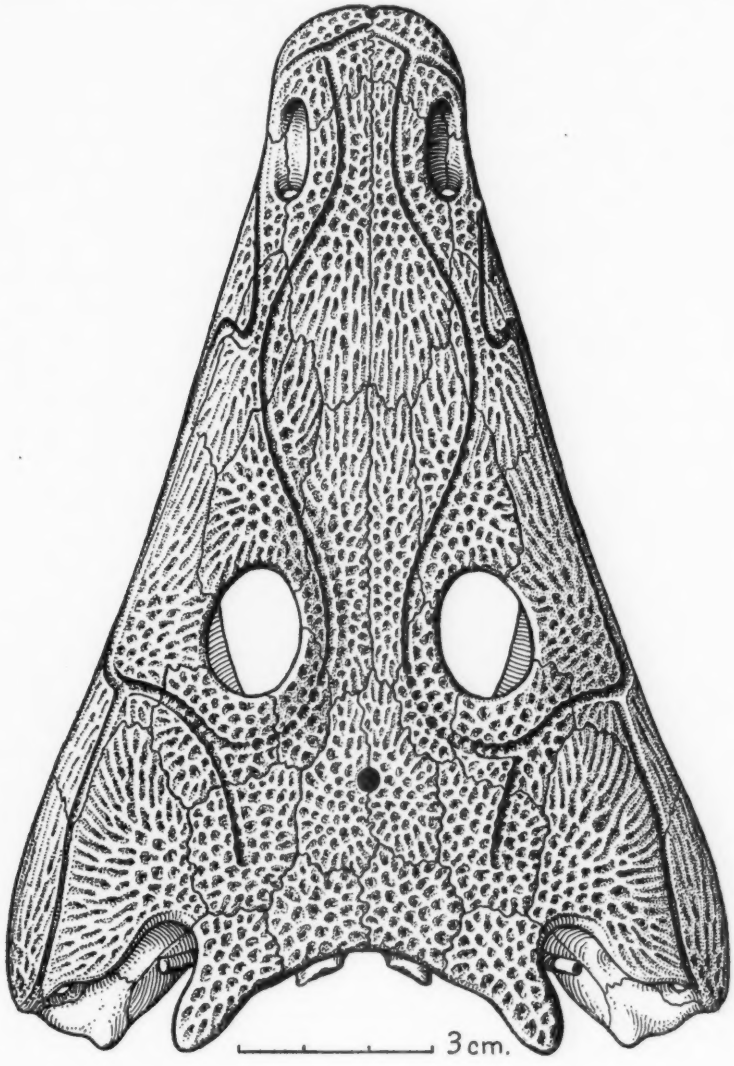

Fig. 3. Benthosuchus sushkini. Dorsal view of skull.

As we know, such representatives of the modern Urodela, as the newts, have seismosensory organs shaped as spheric accumulations of epithelial cells, situated in the superficial portions of the skin only during the summer months, when these amphibians hardly ever leave the water. During the hibernation under stones and roots of trees on land the seismosensory organs of newts sink deeply into the skin and do not function.

These interesting phenomenons are very good proofs of intimate connection between the function of seismosensory organs and the presence of water medium. The same thing is shown by the presence of the seismosensory system organs in neotenic forms of the Urodela, which never have left water, as well as the absence of these organs in the lungless Plethodontidae, living on land.

All the modern Anura (with the exception of Pipidae, Bombina bombina and Ceratophrys laevis) as adults are entirely deprived of a seismosensory system, although it is present in their larvae (NOBLE 1931).

As we know, among the Anura both aquatic and terrestrial forms are to be found; in many typical aquatic forms the seismosensory organs are absent. As to the few representatives of the Anura, which are provided with a seismosensory system, they always prove to be closely connected with water (Pipidae, Bombina bombina, Ceratophrys laevis).

Without a doubt the seismosensory system of the labyrinthodonts did not represent a series of isolated epithelial formations as in modern amphibians but a system of canals the numerous openings of which are distributed on the surface of the skin, so, as we meet in fishes.

The earliest stegocephalians known at present—the upper Devonian Ichthyostegidae—had seismosensory canals passing in the bones of the skull, like in crossopterygians; the openings of these canals are distributed on the surface of these bones (SÄVE—SÖDERBERGH 1932).

Most of the Carboniferous, Permian and Triassic labyrinthodonts have the seismosensory system (in cases when it is present) already in the furrows of the dermal bones; but there is no doubt that—as formerly—it represented a system of canals. Consequently, in these forms it had not yet been reduced to that degree as in the modern amphibians.

All this shows that the labyrinthodonts provided with a seismosensory system were very closely connected with water. Possibly the connection was even closer than that of the modern typical aquatic amphibians.

Thus, the presence of well developed seismosensory canals in Benthosuchus sushkini does not allow us any doubt that it has been in great need of water and represented a typical hydrophilous labyrinthodont.

But besides these canals we have another very important and interesting proof of the hydrophilousness of this labyrinthodont. This proof has been found during the investigation of the microscopic structure of its dermal bones.

I have made a great many transparent sections of all the dermal bones of the Benthosuchus without any exception and discovered a very singular peculiarity of their structure.

In every with sculpture provided dermal bone of any labyrinthodont three layers can be discerned: lower, middle and upper.

The lower layer consists of more or less discernable horizontal lamellae. In this layer canals can be seen, which radially come out of the bone centre, the

VOL
28
194

diameter of the canals being usually very small; some of them must be surrounded by Haversian lamellae; others are deprived of them.

The middle layer represents a series of bone slats and partitions, separating between themselves very large canals, which like the narrow canals of the lower layer radially come out of the bone centre and are directed to its periphery. The walls of these canals are usually formed by the lamellae of the Haversian system. In the middle layer marks can be frequently seen of its multiple reorganization accompanied by the destruction of old Haversian system and by the formation of new ones around the large canals.

The upper layer is formed by numerous curved bone plates, forming on the exterior surface of the bone a round-celled sculpture. Canals pass through this layer directed to the bottom of each cell; vessels, supplying blood to the skin, passed through the canals.

During the growth of the bone a thickening takes place by means of accumulation of new horizontal lamellae on the lower face of the lower layer and by means of simultaneous accumulation of new curved bone lamellae on the outer face of the upper layer. Besides this the successive phases of growth of the thickness of the upper layer have been accompanied by the formation of new sculpture generations. Each new sculpture generation is known to differ from the previous by the larger diameter of the cells and by larger dimensions of combs (Bystrow 1935).

When investigating the upper layer structure in its lower portions it is usually very easy to discover combs of smaller height and cells of smaller diameter, i.e. earlier sculpture generations compared to the sculpture generation forming the surface of the given bone.

At the same time with the growth of thickness of the bone an intensive reorganization of the slats and partitions has taken place in the middle layer of the bone. This reorganization has partially taken place in the upper and lower layers of the bone. In the upper layer it has destroyed the curved lamellae forming the earlier sculpture generations, and in the lower one—the oldest horizontal bone lamellae substituting for both slats and partitions.

This resulted in continuous growth of thickness of the middle bone layer, whereas the thickness of the upper and lower layers remained nearly the same notwithstanding the simultaneous accumulating of new bone lamellae on them.

Such is in general outlines the structure and modifications taking place in the course of growth of the dermal bones in every labyrinthodont and in particular in the Benthosuchus sushkini.

But the dermal bones of the Benthosuchus have an interesting and important peculiarity. The latter consists in the fact, that the upper layer of every dermal bone of this labyrinthodont, which is covered with round-celled sculpture is penetrated by numerous narrow canals. These canals anastomose with each other and form a thick net (fig. 4).

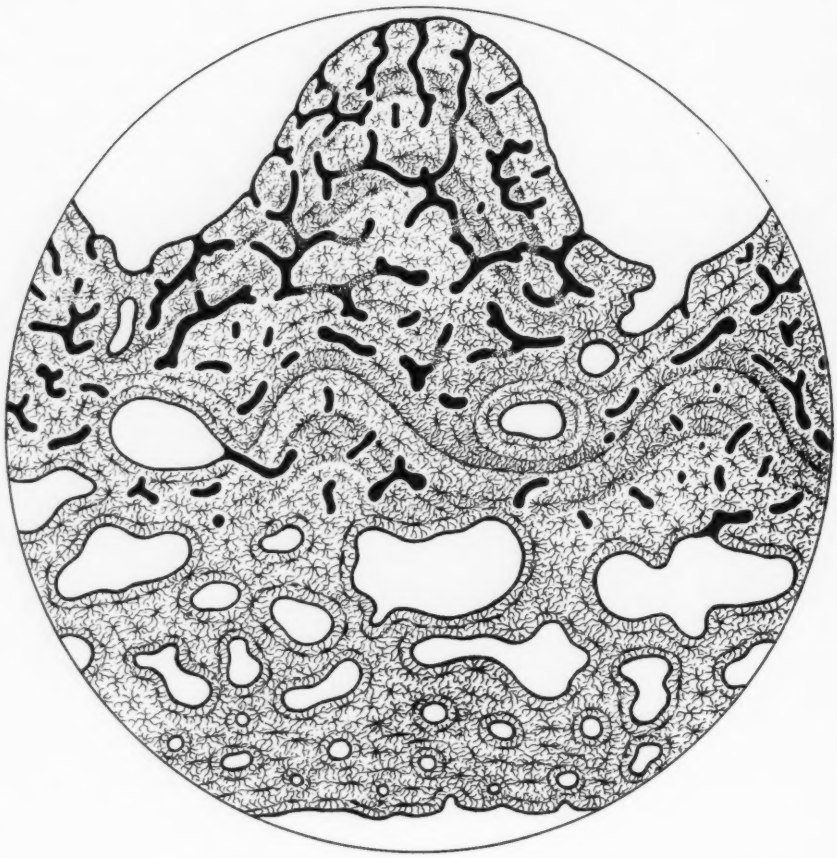

Fig. 4. Benthosuchus sushkini. Vertical section of dermal bone of skull. 100 ×.

This net is especially well seen on horizontal sections, passing through the combs, forming the celled sculpture of the bone (fig. 5).

A detailed investigation of the net made on numerous and various sections has shown that the narrow canals, which form the net, are on one side connected to the large canals of the middle layer, and on the other side by means of numerous small openings to the outer surface of the bone.

The histological study of bones of modern vertebrates is known to have shown, that in every Haversian canal, however, a small artery passes as well as a comparatively big vein, thin branches of nerves and lymphatic vessels.

Therefore I think we have no reason to doubt that in a net of canals penetrating the upper layer of the dermal bones of the Benthosuchus, blood vessels have been present forming a peculiar Rete vasculosum.

VOL
28
194

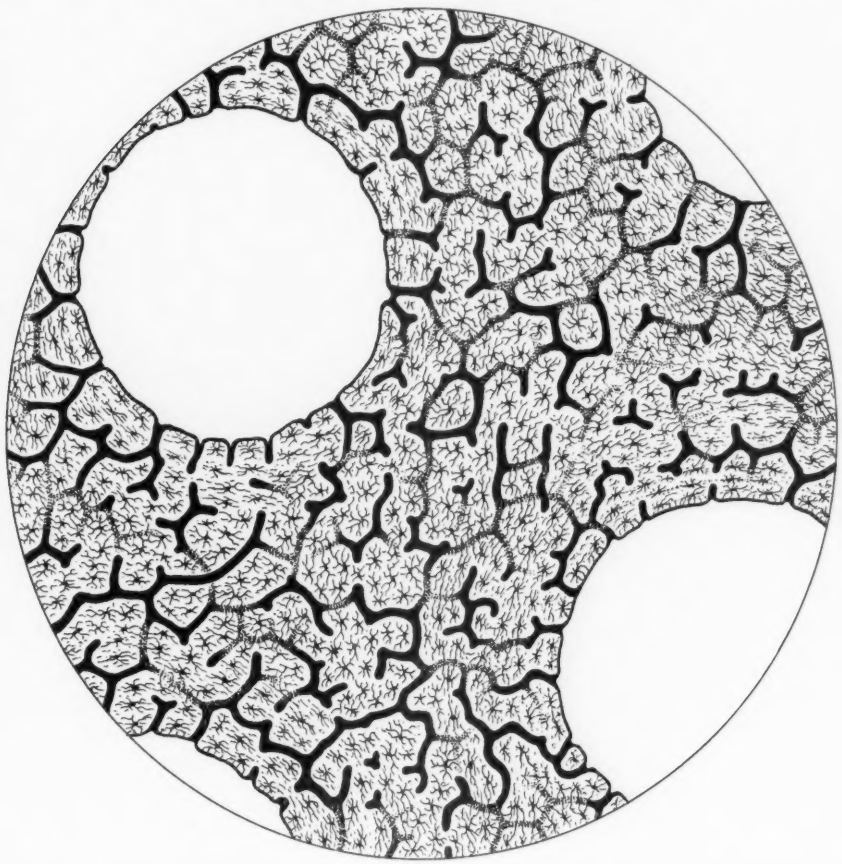

Fig. 5. Benthosuchus sushkini. Horizontal section of dermal bone of skull. 100 ×.

This Rete vasculosum had essentially nothing to do with the bone, and represented the vascular net of the skin. It may be with safety said that coming out through numerous openings on the outer surface of the bone beyond its limits this Rete vasculosum continued further into the skin, while the density remained the same.

It is to be supposed that the vascular net penetrated the upper layer of the bone not for the reason that it was its necessary component, but due to the fact that in the course of the thickening of the bone the accumulation of bone lamellae on its outer surface inavoidably resulted in the fact, that part of the dermal Rete vasculosum was gradually immured in the combs of the sculpture.

Very interesting and important is the fact that round the narrow canals of the vascular net it is hardly possible to discover lamellae of the Haversian systems. The numerous canals of the net penetrate the curved bone lamellae

of the upper bone layer in the most different directions and do not in any place destroy their structure and arrangement.

I never have seen any marks of bone reorganization round the canals of the Rete vasculosum. Consequently, the canals do not change neither their diameter, nor their position during the whole of the animal's life.

An impression is formed that this peculiar vascular net is a kind of extraneous formation for the bone and is evidently intended not for its blood supply. Being immured in the bone, the Rete vasculosum forms nevertheless the vascular net of the skin.

If we imagine the curved bone lamellae, forming the sculpture of the later generations to be removed, and thus make free from the bone the system of canals, we may easily form a clear idea on the number of blood vessels contained in the skin. This vascular system has evidently remained in the skin up to the moment of formation of the last sculpture generations in the combs of which it later proved to be immured.

VOL
28
194

Very important is the fact that the Rete vasculosum exists only in the combs of the celled sculpture of the dermal bones. It is absent in those areas of these bones which are deprived of sculpture; the vascular net is lacking also in the bones, which have no sculpture at all, for instance, in those forming the paletal and occipital part of the skull, as well as in bones situated on the inner face of the lower jaw. This is due to the fact that their surface is not in direct contact with the skin.

This proves once more that the Rete vasculosum is the vascular net of the skin and not of the bone.

I have made a great deal of preparations of all the dermal bones of the Benthosuchus without any exceptions, and I may say with safety, that wherever there exists a round-celled structure, in this labyrinthodont it proves to be penetrated by numerous narrow canals.

A thick net of these canals may be seen not only in all the dermal bones of the skull, having a surface directly covered with skin, but also in sculpture areas of such dermal bones of the shoulder girdle, as Clavicula and Interclavicula.

This proves that in the Benthosuchus the cutaneous vessels are well developed not only in the skin on the head, but also in that, covering the ventral surface of the shoulder girdle.

The absence of dermal bones in other portions of the animal's body does not allow us to prove the presence of the Rete vasculosum outside the head and the region of the shoulder girdle. However, we have no reason to deny the existence of such a vascular net in the skin of the body. It would be very strange indeed if the ample blood supply of the skin was limited by such portions, as the dorsal and lateral surfaces of the animal's head and the ventral surface of its shoulder girdle.

I think the uncommonly great number of vessels in the Benthosuchus' skin may be due only to the very intensive cutaneous respiration, which this labyrinthodont has undoubtedly had.

The number of cutaneous vessels in the Benthosuchus has been so great, that it is necessarily to be supposed this stegocephalian to be like the modern Plethodontidae—lungless and to have the whole of the gaseous exchange accomplished wholly through the integuments.

I think nevertheless we must obstain from this suggestion for the following reasons:

The recent lungless Salamanders are essentially terrestrial forms, and have therefore no organs of the seismosensory system. They do not live in water, but in order to secure a normally functioning cutaneous respiration, they are in need of very damp air. For instance, such a lungless form as the Onychodactylus fischeri lives in very damp places of the East Siberia. This amphibian carefully avoids the sunshine and therefore hides under stones during the whole day. The Onychodactylus comes out only in the night to look for food, which consists of spiders, flies, small snails etc.

VOL. 28 1947

It seems to me that in view of such a mode of life of the lungless ampibians, they may be named "terrestrial hydrophiles".

Evidently the Benthosuchus could not be such a terrestrial hydrophile, for it had a well developed seismosensory system, which proves its close connection with water.

It is to be supposed it never wandered far from the water basins in which its larvae have developed and in which it had got its food. Its seismosensory system organs as well as the vascular net in the skin were equally in need of damp state of integuments. This damp condition has been attained and maintained by means of secretion of the cutaneous glands and the other side of the close connection of the labyrinthodont with water. This connection was one of the necessary conditions, which were indispensable for cutaneous respiration as well as for maintaining the normal functioning of the seismosensory system.

Thus, the Benthosuchus appears to be a labyrinthodont which has lived in very damp places of its living area. It has had need of damp air, like the modern lungless salamanders, having an intensive cutaneous respiration, and has been connected with water, like the newts, which possess seismosensory organs.

The Wetlugosaurus angustifrons, found in the synchronous deposits of the east half of the Russian Platform, had the same peculiarities. This labyrinthodont did not differ from the Benthosuchus sushkini as to the degree of development of its seismosensory system, as well as to the microscopic structure of dermal bones.

Besides skulls and bones of the postcranial skeleton of the Benthosuchus and Wetlugosaurus I have had at my disposal some fragments of bones of various,

frequently not yet defined stegocephalians. The study of them allows me to state that in all the cases where the presence of seismosensory system furrows is accompanied by the presence of a thick net of narrow canals in the sculpturified portions of the dermal bones. Thus these peculiarities are as a rule inseparable. Therefore I think the presence of seismosensory system canals as well as of the Rete vasculosum are to be looked upon as two characteristic features of the hydrophilous labyrinthodonts.

Hence, every labyrinthodont in which we discover well developed furrows of a seismosensory system on the skull and a net of narrow canals in the sculpture combs of the dermal bones, must be acknowledged as a hydrophilous form.

THE XEROPHILOUS LABYRINTHODONTS.

Among the stegocephalians I have investigated there were forms, the skull of which has been deprived of any marks of seismosensory system furrows.

The rhachitomous labyrinthodont Platyops watsoni is to be counted among such stegocephalians. It has been found in the Upper Permian deposits on the Viatka river in 1923 (EFREMOV 1933).

The skull of the Platyops has the shape of a narrow wedge with a small expansion on the front edge. Its total length varied in several specimens from 200 to 300 mm. Old animals had probably still longer and narrower skulls.

The dermal bones of Platyops watsoni's skull are covered with a round-celled sculpture typical for the stegocephalians, but there is an absolute lack of any furrows of seismosensory canals (fig. 6).

This fact alone makes us suppose the Platyops unlike the Benthosuchus, not to be a hydrophilous form.

However, it must be owned that alone the reduction of the system of seismosensory receptors is not sufficient to give us the right to affirm with safety, that the Platyops can be only a terrestrial labyrinthodont; notwithstanding the absence of the seismosensory system—the Rana ridibunda, for instance, is an aquatic form. However, there is no doubt that the Platyops has been adapted to the terrestrial mode of life more than any hydrophilous labyrinthodonts. Nevertheless, it could not wander on great distances from fresh-water basins, for it used them for breeding as well as for getting food. Therefore it is to be supposed that the Platyops has lived on the coasts of rivers and lakes. Furthermore, we have no reason to doubt its skin to be much drier than that of the hydrophilous labyrinthodonts; this peculiarity has been fully due to the fact that it was more adapted to the terrestrial mode of life. We may with safety say this mode of life to be the cause of its seismosensory system reduction.

VOL. 28 194

The study of the microstructure of the dermal bones of the Platyops' skull has fully confirmed the conclusion which could be made only on the base of the fact of this labyrinthodont having no seismosensory system.

Numerous transparent sections, made of dermal bones of this animal's skull have shown that according to structure all these bones do not differ from those of all the other labyrinthodonts, but their upper layer does not contain a net of narrow canals, so well developed in hydrophilous forms (fig. 7).

In the combs of the Platyops, forming the celled sculpture, sometimes isolated small canals are seen, but the number of them is not to be compared to that discovered in the Benthosuchus, Wetlugosaurus and all the other hydrophilous labyrinthodonts.

On horizontal cuts through sculpture combs in the Platyops it is usually possible to find only few narrow canals, therefore the general picture of such cuts very much differs from corresponding cuts of the dermal bones of the hydrophilous forms of labyrinthodonts (fig. 8).

The Platyops has usually one opening on each sculpture cell bottom. Comparatively wide canals through which vessels directed to the skin passed open on the surface of the bone through these openings (fig. 7). These vessels were branches of large vessels, situated in the middle layer of the bone.

The same openings may be seen on the bottom of each cell also in hydrophilous labyrinthodonts.

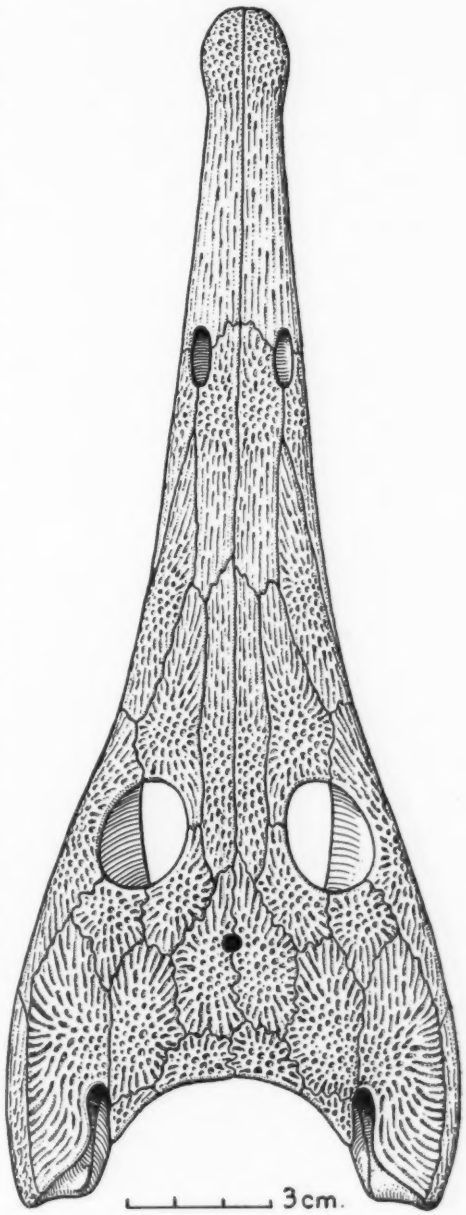

Fig. 6. Platyops watson. Dorsal view of skull.

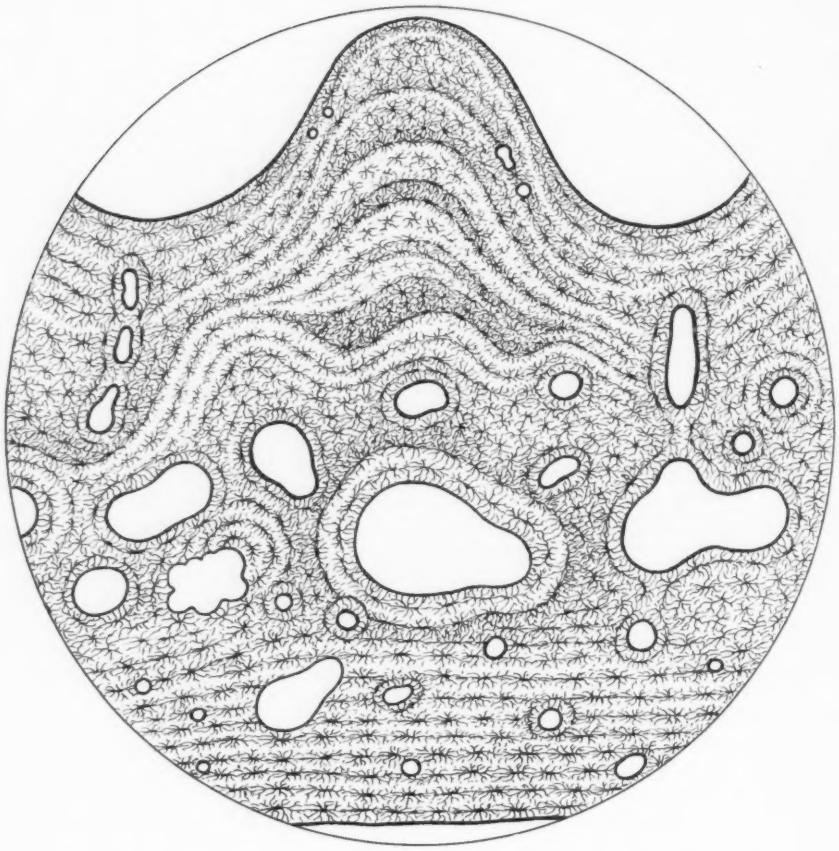

Fig. 7. Platyops watsoni. Vertical section of dermal bone of skull. 100 ×.

Consequently, in this respect the Platyops has been similar to them. At the same time it strongly differed from them, for the upper layer of its bones has been fully deprived of the Rete vasculosum. We must therefore admit the blood supply of the Platyops to have been much poorer. This allows us to conclude its cutaneous respiration has been also much less intensive, than that of the hydrophilous stegocephalians. It is not impossible, that it was nearly absent, or at any rate has not had such an importance for the animal, as for the hydrophilous stegocephalians.

If we admit the good development of the seismosensory system canals, as well as the presence of Rete vasculosum in dermal bones to be an evident proof of any labyrinthodonts having been hydrophilous forms, we must consider the lack of both these formations in the Platyops as a proof of its being a xerophilous form.

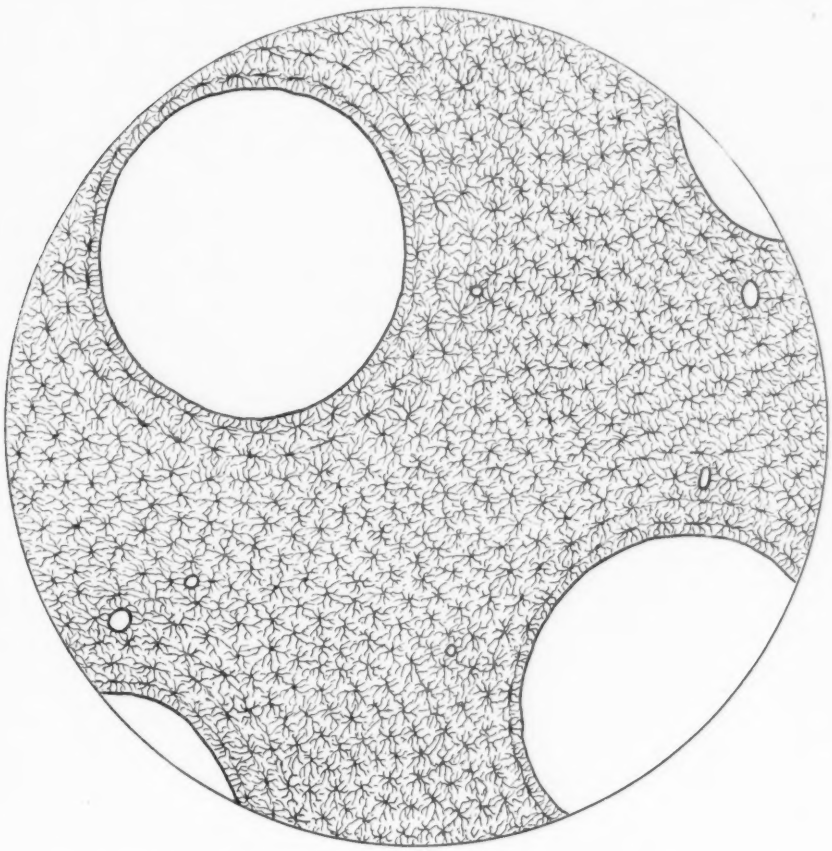

Fig. 8. Platyops watsoni. Horizontal section of dermal bone of skull. 100 ×.

We suppose the Platyops watsoni to be a terrestrial labyrinthodont, which has spent the greater part of its life on the coast of a water basin. It probably used to plunge into water only in order to catch a fish.

The limestone in which numerous fragments of the Platyops have been found was in some places full with scales of Palaeoniscidae. It proves the ichthyofauna of the fresh-water basins on the coasts of which has lived this labyrinthodont to be sufficiently abundant. Therefore it had no need to spend much work in order to get food. Besides this, the Platyops has undoubtedly been a good strong swimmer, and its long jaws armed with sharp teeth, allowed to seize the live prey easily and quickly.

Besides the Platyops watsoni I have had at my disposal the skulls of upper-permian labyrinthodonts Platyops stuckenbergi, Melosaurus sp., skull fragments

of the Enosuchus breviceps and broken pieces of dermal bones and several indeterminable forms.

All of them have no seismosensory system furrows; at the same time the net of narrow canals in the sculpture combs has also been lacking.

Thus, we may say that in all the cases when the seismosensory system has been subject to full reduction, the labyrinthodont proved to be deprived also of the Rete vasculosum.

Hence the absence of seismosensory system furrows on the skull as well as of a thick net of canals in the dermal bones sculpture represent two peculiarities which are connected with each other.

I think we have no ground to doubt both these peculiarities to be features of xerophilousness. Therefore, every labyrinthodont lacking both these formations must be acknowledged to represent a xerophilous form.

The hydrophilous and xerophilous labyrinthodonts seem to represent two extreme types of adaptation to the aquatic and the terrestrial mode of life. It is however possible that a detailed investigation of stegocephalians known at present will allow to state a series of intermediate or transitional forms between the typical hydrophiles and xerophiles. We have no reason to doubt such labyrinthodonts to have existed.

Besides this it may be said beforehand, they must have been characterized by an incomplete reduction of the seismosensory system of canals and by a comparatively small development of the Rete vasculosum in the dermal bones sculpture.

THE HYPERHYDROPHILOUS OR NEOTENIC LABYRINTHODONT.

Among the various forms of the labyrinthodonts, investigated by me, the most interesting is without any doubt the Dvinosaurus, found in 1899 in the Upper Permian deposits on the North Dvina (Amalitzky 1924, Efremov 1931, Sushkin 1936, Bystrow 1938).

The Dvinosaurus' skull is short and broad, its length varies between 159 and 198 mm; the orbits are comparatively large, whereas the nasal openings and choanae are small.

This rhachitomous labyrinthodont is similar to all the representatives of the hydrophilous stegocephalians by having very well pronounced seismosensory system furrow (fig. 9). On the bottom of these comparatively broad and deep furrows in many places openings can be seen, which served as points, where the branches n. facialis came out to the receptory apparatus of the seismosensory system.

On some skulls of the Dvinosaurus the seismosensory system furrows form in their course small curvatures (fig. 9). This has resulted in their total length

VOL 28 194

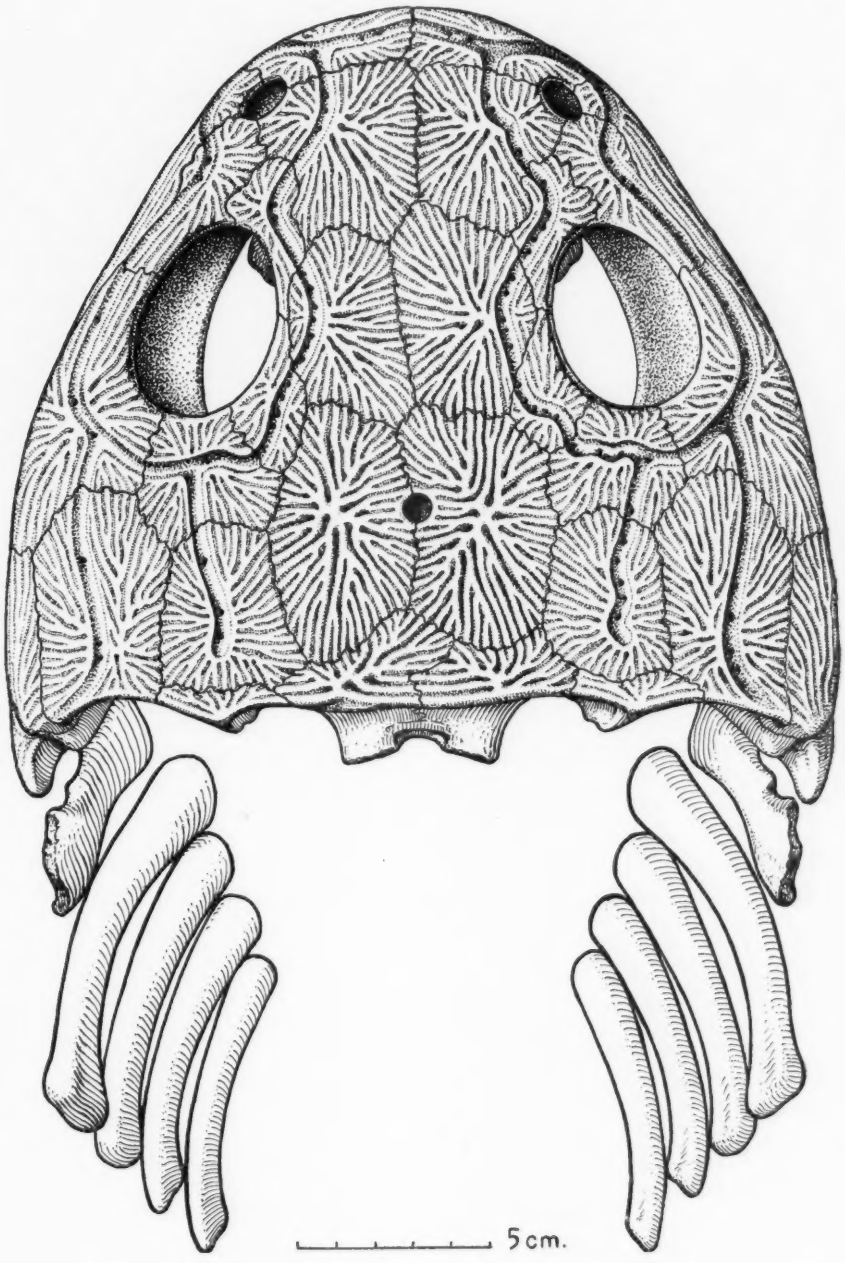

Fig. 9. Dvinosaurus Amalitzky. Dorsal view of skull.

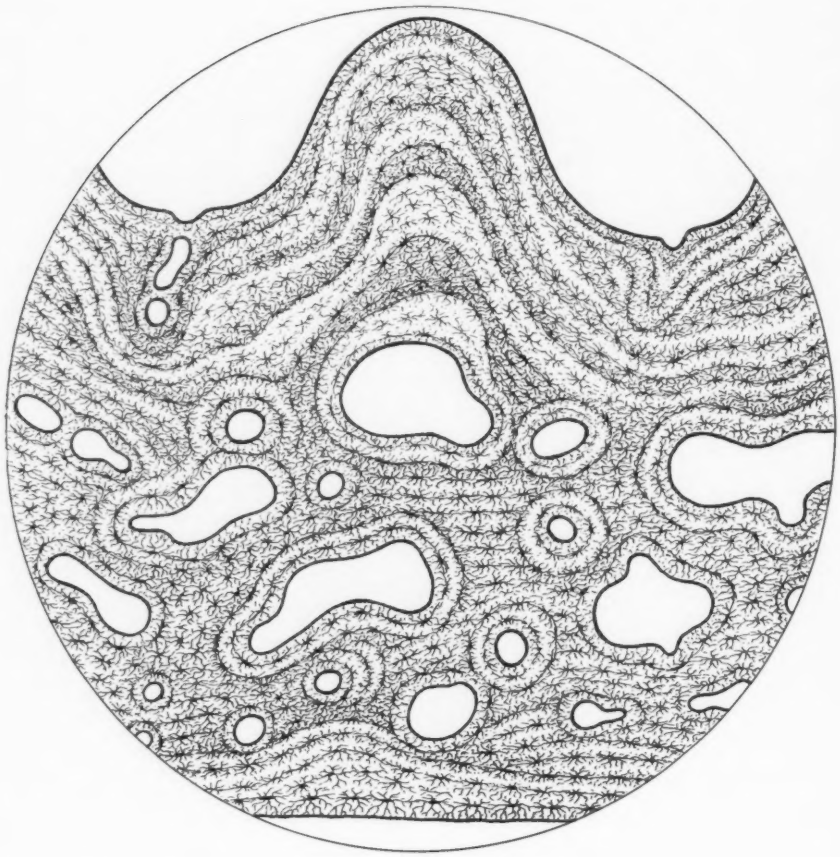

Fig. 10. Dvinosaurus. Vertical section of dermal bone of skull. 100 ×.

being greater than it would be, had they been going without these curvatures from the punctum ossificationis of one bone to that of the other, as it is usually observed in labyrinthodonts.

A good development of the seismosensory system undoubtedly shows that the Dvinosaurus has been an aquatic form; like the typical hydrophilous labyrinthodonts it has been very closely connected with water and its seismosensory system has undoubtedly been a very important receptory apparatus.

Thus, considering the presence of the seismosensory system furrows, we must admit this labyrinthodont to have been a hydropyhilous form.

However, after having investigated the microstructure of the dermal bones of its skull, we shall form quite a different conclusion. This investigation has shown the net of narrow canals, present in hydrophilous forms, is fully absent

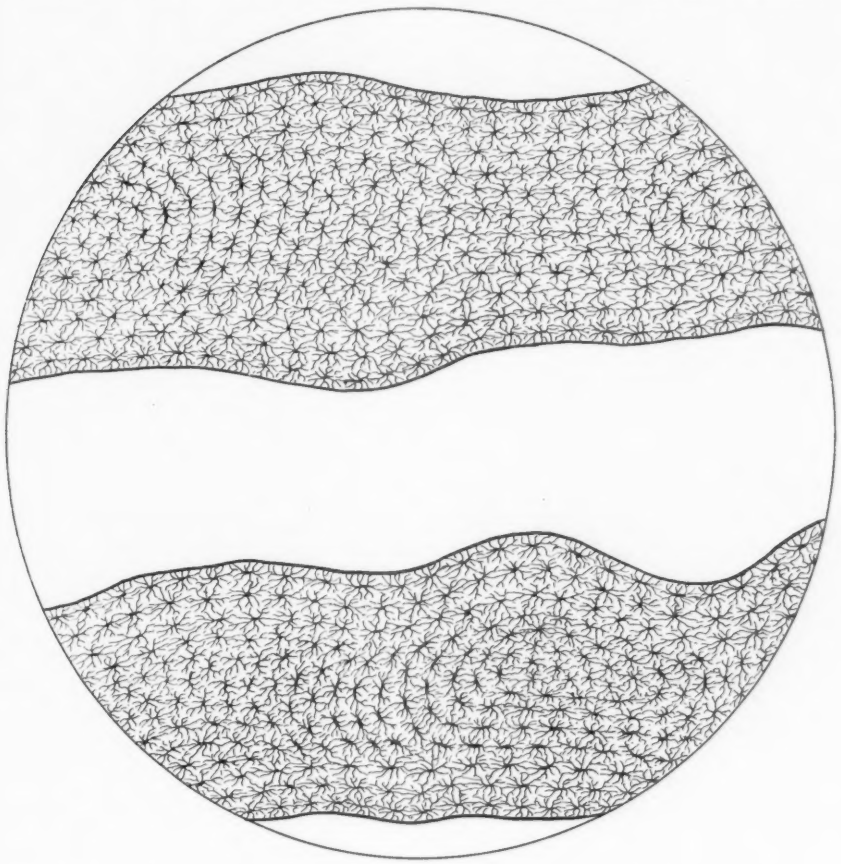

Fig. 11. Dvinosaurus. Horizontal section of dermal bone of skull. 100 ×.

in these bones. This may be clearly seen on the vertical (fig. 10), as well as on the horizontal cuts of the bones (fig. 11).

Between the combs of the dermal bones sculpture of the Dvinosaurus in many places numerous canals are open through which blood vessels come to the skin of the head.

Such canals, as we have seen, are present also in the dermal bones of the xerophilous labyrinthodonts (fig. 7). In this respect the Dvinosaurus is similar to them and the blood supply of its skin has not been richer than in such forms as the Platyops, Melosaurus and Enosuchus.

Hence, as to the structure of its dermal bones, the Dvinosaurus has not differed from the xerophilous labyrinthodonts.

Thus we observe in this peculiar labyrinthodont a simultaneous presence of two features, having contrary meanings, namely: the features of hydro-

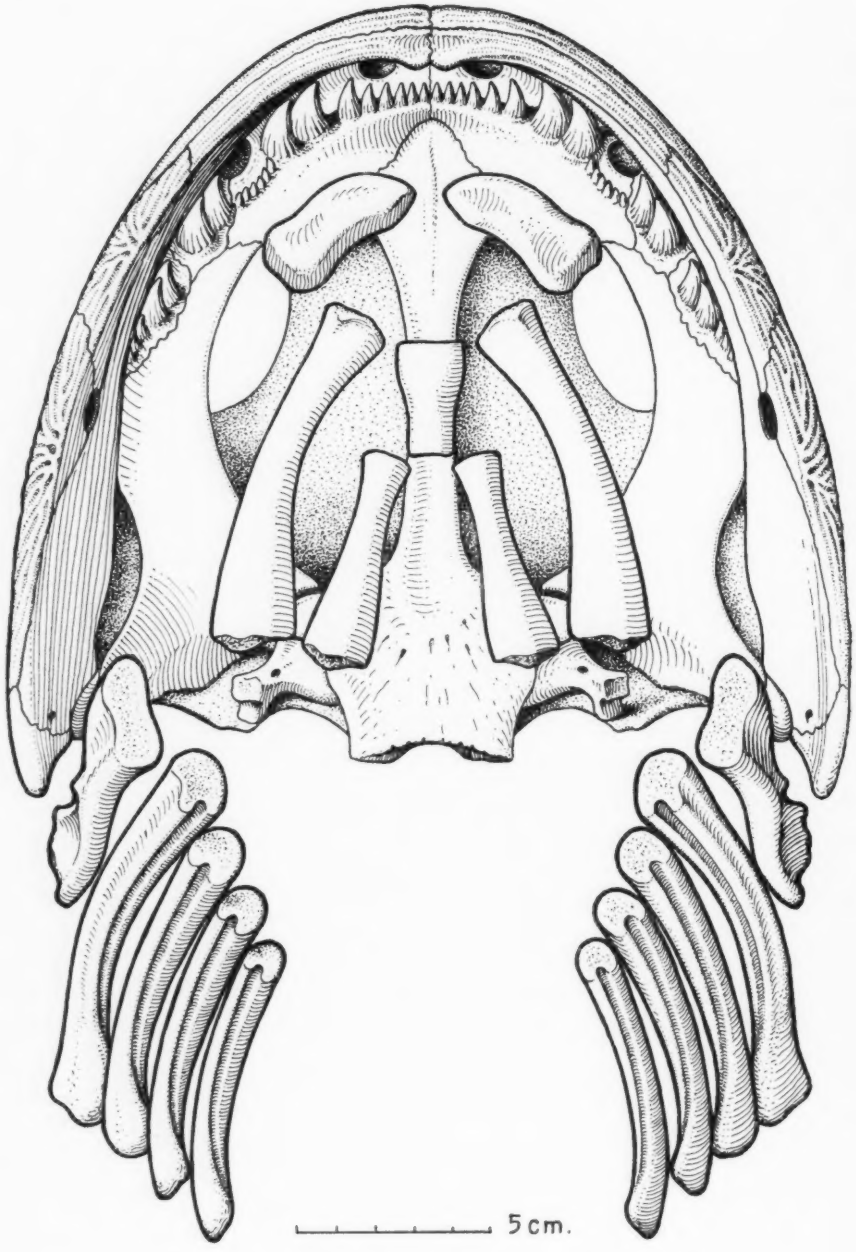

Fig. 12. Dvinosaurus Aamalitzky. Ventral view of skull.

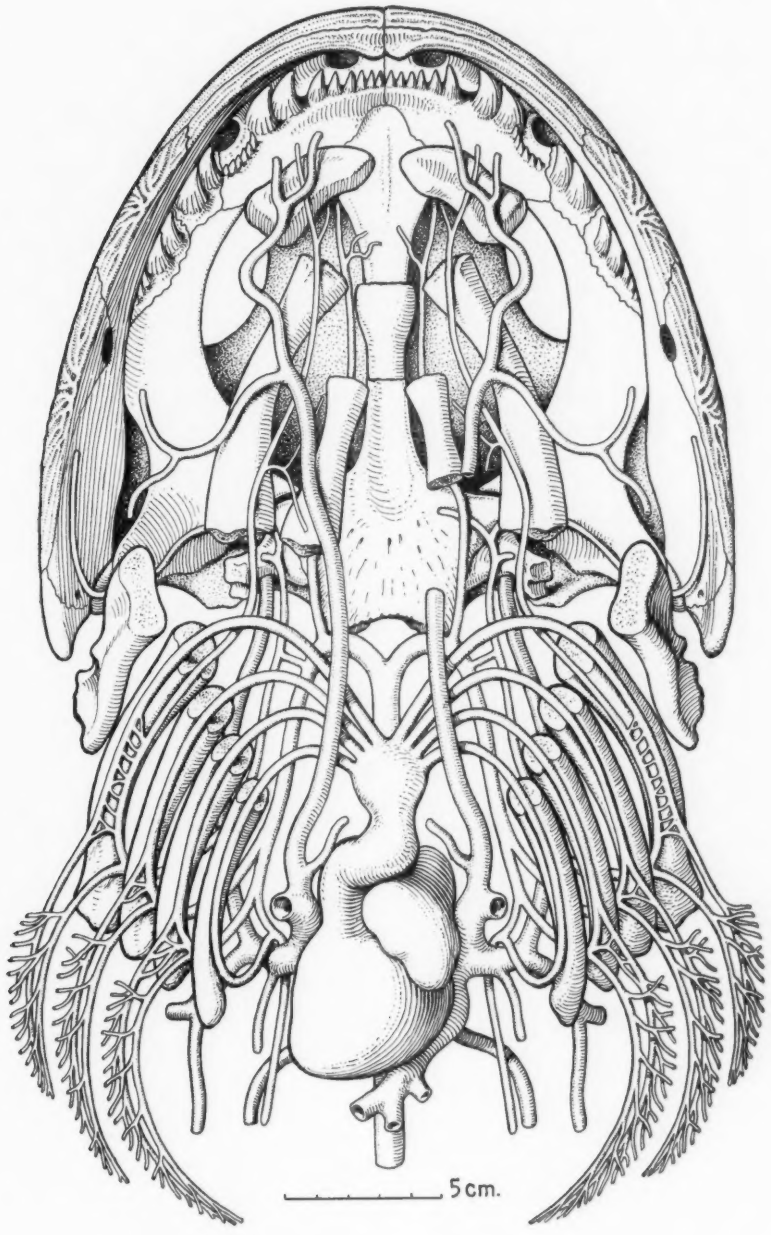

Fig. 13. Restoration of blood-vessels of head in Dvinosaurus.

philousness (the presence of the seismosensory system) and the feature of xerophilousness (the presence of the Rete vasculosum).

Such a combination of features seems to contradict everything we have said about the peculiarities characterizing the hydrophilous and xerophilous forms. Undoubtedly the Dvinosaurus would represent an unsolvable problem for us if we were acquainted with it only on the ground of the few skull fragments. Luckily we know it on the ground of a nearly complete skeleton and a sufficient number of complete skulls. When investigating this material, very well ossified elements of a hyobranchial apparatus has been discovered, which allowed us to state without any doubts that the Dvinosaurus has represented a neotenic form of the labyrinthodont.

It had not undergone any metamorphosis and, like the Necturus maculosus, Siren lacertina, Proteus anguinus, Typhlomolge rathbuni of the living Urodela, had a life-long retention of gill-breathing. As a larva this labyrinthodont has been up to 150 cm long.

It is quite naturally, that this has strongly influenced many peculiarities of its skeleton's structure and especially the dermal bones of its skull. No round-celled sculpture, which is typical for all the labyrinthodonts, has developed on these bones. Instead of it long high combs have developed which have gone radially from the centre of the bone to its rims (fig. 9). Evidently these combs have resulted from a strong hyperplasia of larval sculpture of bone. The hyobranchial apparatus of the Dvinosaurus as to the number, position and shape of bones does not differ very much from the corresponding apparatus of the larvae of all the modern Urodela (fig. 12).[1]

This striking resemblance allows to restore positively the vessel system of his head and to count, that this labyrinthodont had three external gills as the larvae of all modern Urodela (fig. 13).

The doubtless fact that the Dvinosaurus in the course of his life remained as a larva, brings us to the conception, why he had a well developed seismosensory system and why the Rete vasculosum in the sculpture of his dermal bones was absent.

The seismosensory system characteristic for the larvae of the amphibians, has naturally remained in it, for it had not undergone any metamorphosis. Besides the function of this system was very important for it, as it never left and never could leave the fresh-water basins, in which it lived.

The gaseous exchange in the Dvinosaurus has been executed by means of gills and their function, like that of the fishes has been quite sufficient for

[1] A study of a new find of incomplete and broken skeletons of the Dvinosaurus from the Upper Permian deposits on the Volga allows me to make some corrections in the reconstruction of the hyobranchial apparatus of this labyrinthodont, previously published by me (Acta Zoologica, 1938, Bd. 19; 1939, Bd. 20).

Besides this, I consider it necessary to say that numerous studies of skulls of Dvinosaurus and additional preparation of them makes it now possible for me to say with safety that this labyrinthodont has an opening in the stapes.

VOL
28
194

supplying the organism with the necessary amount of oxygen. At the same time the cutaneous respiration has been very difficult for this labyrinthodont, for it required a much more considerable amount of oxygen, than that, contained in the water (30 times less than the amount contained in air). The gaseous exchange through the integuments did not, evidently, take place. This resulted in the fact, that its dermal bones as to their structure proved to be similar to the bones of the xerophilous labyrinthodonts.

As the Dvinosaurus has been an enormous gill-breathing larva, it never came out on land. It probably has hidden in the thick growth of water-plants, waited for its prey, and remained quite without moving for a long time—to say nothing of the vibration of its gills.

According to the dimensions of the orbits the Dvinosaurus has big eyes, which made it possible for it to see even in places, where the day-light hardly penetrated.

Springing suddenly at the by-swimming fishes it seized its prey with its wide jaws, armed beside numerous small conic teeth, also with very big sharp tusks.

It is probable that like the neotenic modern Urodela, the Dvinosaurus had primitively built lungs, which, however, have hardly taken considerable part in the gaseous exchange. Nevertheless it has been obliged to change periodically the air in them. For that end it rose from time to time to the surface of the water, let quickly out the used-up air, and, having taken a new portion of it, has slowly sunk to the bottom of the basin to remain again without moving during a long time...

Such a peculiar stegocephalian as the Dvinosaurus may be named a hyper-hydrophilous form, for it has been connected with water much more than any of the typical hydrophilous labyrinthodonts.

At the present time the Dvinosaurus is so far the only labyrinthodont, for which the neotenic condition may be considered quite proved. However, we cannot deny that similar forms may have existed in other areals and in other times (see, for instance, NILSSON 1946).

CONCLUSIONS.

The study of the geographic distribution of modern amphibians has shown, that usually the most various forms may live in the same area. For instance, such representatives of the Anura, as the aquatic Bombina bombina and Rana ridibunda and terrestrial toads live in many cases in the same area, whereas each of these forms finds such areas, in which all their requirements to the environ prove to be satisfied.

Most interesting in this respect is the fauna of North America.

In the eastern part of the USA an enormous region is inhabited by two

kinds of newts, Triturus viridescens and Triturus dorsalis, which as typical representatives of the Urodela, undergo all the stages of the metamorphosis and as adults breathe through the lungs. They spend the greatest part of their life in water, when they get their food.

In the same region of the USA live various representatives of the family Plethodontidae (Plethodon, Eurycea, Typhlotriton, Desmognathus, Leurognathus, Hemidactylium, Aneides and so on). As adults all of them are terrestrial forms and are lungless. Their gaseous exchange is accomplished through the skin and the mucous membrane of the mouth cavity. This requires humid air, therefore the Plethodontidae, in search of the dampest places, usually hide under stones and roots of trees. They do not live in water and therefore are deprived of a seismosensory system. If during the daytime the lungless amphibians are obliged to remain under stones, in the night they become more active and got their food only on land.

In the same eastern half of the USA, but on smaller areas, live such neotenic forms of the Urodela, as the Necturus and Siren. These amphibians, as we know, do not undergo any metamorphosis; during their whole life they have a gillbreathing and never have left the water basins they get their food in.

Thus, the areas occupied by these various forms cover each other to a great extent. In addition to this the climate difference existing between the northern and southern parts of the eastern half of the USA, do not seem to influence these amphibians. This can be seen, for instance, on the distribution of the Necturus, which lives in rivers on the area from the Great Lakes to Louisiana.

All this has shown that such ordinary Urodela, as newts, as well as such gill-breathing forms as the Necturus and the Siren, and such peculiar amphibians as the lungless Plethodonthidae with equal ease find convenient dwelling places in this vast area.

On the ground of this fact we must suppose that also in the past hydrophilous and xerophilous labyrinthodonts could occupy the same area. However, such a solution of the problem we are interested in, meets with some difficulties. Both kinds of stegocephalians have lived on fish and therefore have been equally in need of water basins. Hence, living in a common areal, they had to obtain food in the same rivers and lakes and thus live in intimate contact with each other. Besides this, the xerophilous forms which have had a comparatively dry skin and have been deprived of a seismosensory system, have been fully adapted to the terrestrial mode of life, while the hydrophilous forms having a well developed seismosensory system and being capable of an intensive cutaneous respiration have been obliged like the modern Plethodontidae to hide under stones at least during the whole of the daytime.

I suppose that considering the dimensions of many hydrophilous labyrinthodonts, such mode of life must be thought improbable. If the small

VOL
28
194

Plethodontidae of North America and the Onychodactylus fischeri of East Siberia can find retired nooks, where humid air lasts nearly during the whole day, the search of similar places for such big hydrophiles as the Benthosuchus and the Wetlugosaurus would undoubtedly be at least difficult.

In addition to this it is necessary to have in view that, if we admit, the hydrophilous labyrinthodonts to have remained without moving during the whole day under stones on roots of trees, we must also admit they have caught fish ... only in the night. This appears to be still more impossible.

Both the hydrophilous and xerophilous labyrinthodonts have been undoubtedly day beasts of prey. For the reason of their absolutely opposite peculiarities they evidently could not with equal ease find in the same areal convenient conditions for their existance. It was especially hard for the hydrophilous forms, for with a common macroclimate, which could fully satisfy the xerophilous forms, they had to look for such places, the microclimate of which made possible their existance in the same areal.

On the ground of all these facts we must admit that the common influence of the climate on the big labyrinthodonts should have been much stronger than the influence produced by the climate on the small modern amphibians. It seems that the following statement must be admitted to be correct: the smaller are the dimensions of the animals, the easier they find such dwelling places, the microclimate of which makes their existence possible, notwithstanding the macroclimate of the areal being in general unfavourable for them.

Similarly the greater the dimensions of the animals, the harder for them the existence in comparatively unfavourable conditions. Thus, the bigger animals depend on the climate much more than the small ones. This statement is known to be confirmed by numerous observations of the modern fauna.

The hydrophilous and xerophilous forms of labyrinthodonts have undoubtedly been such forms of fossil amphibians, which have been adapted to quite different macroclimate peculiarities.

Besides this, the hydrophiles have been in need of very great relative humidity of the air, while the xerophiles could easily endure a comparatively dry climate.

Having all this in view, we have to acknowledge, that in areals with arid climate in which the xerophilous labyrinthodonts could live, the existence of hydrophilous labyrinthodonts has been at the least difficult. However, we cannot say the xerophiles could not dwell there, where the hydrophilous forms lived. The relatively humid climate could not, of course, be an obstacle to the existence of such terrestrial forms as the xerophilous stegocephalians.

Therefore we seem to be obliged to admit the hydrophilous labyrinthodonts to be a more reliable indicator of the climate, than the xerophilous ones.

The study of the paleogeographic distribution and chronological interrelations of all the labyrinthodonts I have at my disposal has given the following interesting results.

Labyrinthodonts found in the Upper Permian and Lower Triassic deposits of the basins of the North Dvina and Volga have been used as material for the present investigation. All the Upper Permian forms which have been known to me (Melosaurus sp., Platyops stuckenbergi, Enosuchus breviceps, Platyops watsoni) have proved to be typical xerophiles. A later Upper Permian labyrinthodont Dvinosaurus represented a neotenic form and seemed to be the only representative of the stegocephalians in the end of the Permian period on the territory of the eastern half of the Russian Platform. All of the eotriassic labyrinthodonts without exceptions proved in the same region to be hydrophilous forms.

This allows us to suppose the climate in the eastern half of the Russian Platform to have been relatively dry during the Upper Permian period. Besides, if the Dvinosaurus has really been the only stegocephalian in the end of the Permian period, its neotenic condition is to be considered as an indicator of an increase of climate aridity in the very end of the Permian period.

The presence of a great number of hydrophilous labyrinthodonts in the eotriassic seems to indicate relatively humid climate during this period.

Such are the conclusions resulting of the small material available for us at the present time. However, we have no reason to insist on the absolute correctness of all these most important statements. At present we may say that so far we do not know a single typical hydrophile from the Upper Permian deposits in the eastern half of the Russian Platform as well as any xerophiles from the eotriassic deposits of the same region. This of course cannot mean, that we may with safety affirm that in the Upper Permian there were no hydrophiles and in the eotrassic no xerophiles. It is to be remembered that negative data have no great value in the paleontology.

It is quite clear that if a single hydrophilous labyrinthodont is discovered in the Upper Permian deposits of the Russian Platform we shall be at once obliged to give up the assumption of the dry climate for the end of the Permian, and we shall have acknowledged it to be sufficiently humid. In this case all the Permian xerophilous labyrinthodonts will prove to be only terrestrial forms, which are more adapted to a long sojourn on land than the hydrophilous stegocephalians.

As to possible find of xerophilous labyrinthodonts in the eotriassic, it will not change our opinion about the climate of that period, for, hydrophilous forms being present, the xerophilous stegocephalians cannot be considered as reliable indicators of the climate in the past.

To conclude I think it necessary to underline that both the xerophilous and hydrophilous labyrinthodonts as to their mode of life, undoubtedly have considerably differed from the modern amphibians. No labyrinthodont has in that respect been like any representative of the recent Anura, or Urodela. There-

VOL
28
194

fore to pass judgment on the peculiarities of the climate in the past on the ground of these fossil forms is no easy task.

To what extent the stegocephalians have differed from the modern amphibians can be seen from the following comparison.

As the xerophilous labyrinthodonts had no intensive cutaneous respiration they were similar to newts, but differed from them by a full absence of the seismosensory system. Therefore they have been terrestrial forms to a greater extent than the newts. However, considering the fact, that their food may have consisted only of fish, we must at the same time admit their close connection with water. And this connection has undoubtedly been closer than in any terrestrial form of modern amphibians feeding on insects.

The hydrophilous labyrinthodonts, having a very intensive gaseous exchange through the integuments, have in that respect been like the terrestrial lungless salamanders. However, unlike them, they have had a very well developed seismosensory system, which proves their close connection with water basins. The hydrophilous labyrinthodonts have undoubtedly got their food only in water like the modern newts. Thus, we discover the simultaneous likeness of the hydrophiles with lungless salamanders and with newts.

The only labyrinthodont, whose mode of life does not rouse any doubts, is the Dvinosaurus. We may say with full safety, that in many respects it has had a striking likeness to the neotenic forms of the modern Urodela.

VOL. 28 1947

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VOL
28
194

VOL.
28
1947

THE CRANIAL DEVELOPMENT OF CERTAIN ETHIOPIAN "INSECTIVORES" AND ITS BEARING ON THE MUTUAL AFFINITIES OF THE GROUP

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(With 69 text-figures.)

CONTENTS.

PART I. SUNCUS ORANGIAE (*Roberts*)

I. Introduction and acknowledgments 169
II. Material and technique 174
III. The chondrocranium 175
A. The central stem 175
1. Foramina in the central stem 178
2. Early development of the central stem 178
3. Post optimal changes in the central stem 181
B. Lateral structures appended to the central stem 182
1. The exoccipital cartilages 182
a. Early development of exoccipital cartilages 183
b. Post optimal changes in exoccipital cartilages 184
2. The auditory capsule 184
a. Foramina in the wall of the auditory capsule 189
b. The interior of the auditory capsule 191
c. Early development of the auditory capsule 192
d. Post optimal changes in the auditory capsule 193
3. The ala temporalis 196
a. Early development of the ala temporalis 196
b. Post optimal changes in the ala temporalis 197
4. The ala orbitalis 198
a. Early development of the ala orbitalis 202
b. Post optimal changes in the ala orbitalis 202
5. The nasal capsule 205
a. Early development of the nasal capsule 222
b. Post optimal changes in the nasal capsule 225
C. The dorsal structures 231

IV. The dermal bones 232
A. The premaxilla 232
B. The maxilla 233
C. The lacrimal bone 234
D. The jugal 234
E. The palatine 234
F. The vomer 235
G. The pterygoid 236
H. The nasal 237
I. The frontal 238
J. The parietal 238
K. The squamosal 239
L. The tympanic (ectotympanic) 239
M. The gonial (prearticular) 240
N. The interparietal 240

V. Summary 240
a. The central stem 240
b. Exoccipital cartilages 241
c. Auditory capsule 241
d. Ala temporalis 242
e. Ala orbitalis 243
f. Nasal capsule 243
g. Supraoccipital cartilage 244
h. Dermal bones 245

VOL
28
194

PART II. ELEPHANTULUS MYURUS JAMESONI (*Chubb*)

I. Introduction 246

II. Material and technique 246

III. The chondrocranium 247
A. The central stem 247
1. Foramina in the central stem 248
2. Early development of the central stem 249
3. Post optimal changes in the central stem 250
B. Lateral structures appended to the central stem 251
1. The exoccipital cartilages 251
a. Early development of exoccipital cartilages 251
b. Post optimal changes in exoccipital cartilages 252
2. The auditory capsule 252
a. Foramina in the wall of the auditory capsule 255
b. Early development of the auditory capsule 258
c. Post optimal changes in the auditory capsule 258
3. The ala temporalis 259
a. Early development of the ala temporalis 260
b. Post optimal changes in the ala temporalis 260
4. The ala orbitalis 261
a. Early development of the ala orbitalis 261
b. Post optimal changes in the ala orbitalis 262
5. The nasal capsule 262
a. Early development of the nasal capsule 262
b. Post optimal changes in the nasal capsule 263
C. The dorsal structures 263
1. Early development of the tectum posterius 264
2. Post optimal changes in the tectum posterius 264

IV. The membrane bones 264
A. The premaxilla 264
B. The maxilla 265
C. The lacrimal bone 265
D. The jugal 266

E. The palatine 266
F. The vomer 267
G. The pterygoid 268
H. The nasal 270
I. The frontal 270
J. The parietal 271
K. The squamosal 271
L. The tympanic (ectotympanic) 272
M. The gonial (prearticular) 272
N. The interparietal 272

V. Summary 273
a. The central stem 273
b. Exoccipital cartilages 273
c. Auditory capsule 274
d. Ala temporalis 275
e. Ala orbitalis 275
f. The supraoccipital cartilage 276
g. Membrane bones 276

VOL.
28
1947

PART III. EREMITALPA GRANTI (*Broom*)

I. Introduction 277

II. Material and technique 278

III. The chondrocranium 279

A. The central stem 279
1. Early development of the central stem 282
2. Post optimal changes in the central stem 284

B. Lateral structures appended to the central stem 285
1. The exoccipital cartilages 285
a. Early development of exoccipital cartilages 287
b. Post optimal changes in exoccipital cartilages 288
2. The auditory capsule 288
a. Foramina in the wall of the auditory capsule 290
b. The interior of the auditory capsule 292
c. Early development of the auditory capsule 293
d. Post optimal changes in the auditory capsule 293
3. The ala temporalis 296
a. Early development of the ala temporalis 296
b. Post optimal changes in the ala temporalis 296
4. The ala orbitalis 297
a. Early development of the ala orbitalis 298
b. Post optimal changes in the ala orbitalis 298
5. The nasal capsule 300
a. Early development of the nasal capsule 308
b. Post optimal changes in the nasal capsule 310

C. The dorsal structures 312
1. Early development of the supraoccipital cartilages 312
2. Post optimal changes in the supraoccipital cartilages 312

IV. The membrane bones 313
A. The premaxilla 313
B. The maxilla 314
C. The lacrimal bone 315
D. The jugal 316
E. The palatine 316
F. The vomer 316
G. The pterygoid 317
H. The nasal 317
I. The frontal 318
J. The parietal 318

K. The squamosal . . . 318
L. The tympanic (ectotympanic) . . . 319
M. The prearticular (gonial) . . . 319
N. The tabular and interparietal . . . 319

V. Summary . . . 320
a. The central stem . . . 320
b. Exoccipital cartilages . . . 320
c. Auditory capsule . . . 321
d. Ala temporalis . . . 321
e. Ala orbitalis . . . 322
f. Nasal capsule . . . 322
g. Supraoccipital cartilage . . . 323
h. Membrane bones . . . 323

PART IV. SETIFER SETOSUS (*Schreb.*)

I. Introduction . . . 324

II. Material and technique . . . 325

III. The chondrocranium . . . 326
A. The central stem . . . 326
1. Early development of the central stem . . . 327
2. Post optimal changes in the central stem . . . 330
B. Lateral structures appended to the central stem . . . 331
1. The exoccipital cartilages . . . 331
a. Early development of exoccipital cartilages . . . 332
b. Post optimal changes in exoccipital cartilages . . . 333
2. The auditory capsule . . . 335
a. Foramina in the wall of the auditory capsule . . . 337
b. The interior of the auditory capsule . . . 338
c. Early development of the auditory capsule . . . 338
d. Post optimal changes in the auditory capsule . . . 339
3. The ala temporalis . . . 340
a. Early development of the ala temporalis . . . 340
b. Post optimal changes in the ala temporalis . . . 340
4. The ala orbitalis . . . 342
a. Early development of the ala orbitalis . . . 344
b. Post optimal changes in the ala orbitalis . . . 344
5. The nasal capsule . . . 345
a. Early development of the nasal capsule . . . 353
b. Post optimal changes in the nasal capsule . . . 354
C. The dorsal structures . . . 355
1. Early development of the supraoccipital cartilage . . . 355
2. Post optimal changes in the supraoccipital cartilage . . . 355

IV. The membrane bones . . . 356
A. The premaxilla . . . 356
B. The maxilla . . . 356
C. The jugal . . . 357
D. The lacrimal bone . . . 357
E. The vomer . . . 358
F. The palatine . . . 358
G. The pterygoid . . . 358
H. The nasal . . . 359
I. The frontal . . . 359
J. The parietal . . . 359
K. The squamosal . . . 359
L. The interparietal . . . 360
M. The tympanic (ectotympanic) . . . 360
N. The prearticular (gonial) . . . 360

VOL 28 194

V. Summary 361
a. The central stem 361
b. Exoccipital cartilages 361
c. Auditory capsule 362
d. Ala temporalis 362
e. Ala orbitalis 363
f. Nasal capsule 363
g. Supraoccipital cartilage 364
h. Membrane bones 364

PART V. DISCUSSION OF THE RESULTS OBTAINED IN PREVIOUS PARTS OF THIS PAPER

I. Introduction 365
II. Specific morphological considerations 365
1. The prechordal region of the central stem 365
2. Chondrification and ossification of the auditory capsule 368
3. The "opercular" process and "tabular" 368
4. Ossification of the central stem (basi-cranial axis) 370
5. The anterior paraseptal cartilage 376
6. The ethmoid 377
7. The jugal 378
III. Taxonomic considerations 379
1. Suncus orangiae and Setifer setosus 379
2. Eremitalpa granti 382
3. Elephantulus myurus jamesoni 384
IV. References 388
V. Key to lettering 393

VOL. 28 1947

PART I. SUNCUS ORANGIAE (ROBERTS).

I. INTRODUCTION AND ACKNOWLEDGMENTS.

The Classification of the Insectivores is still uncertain despite repeated contributions from distinguished workers. Before any finality can be reached, however, it is necessary that the embryology and comparative anatomy of the various problematic groups be known in greater detail, and to that end this paper is merely a contribution.

For a review of the earlier taxonomic history of this group the reader is referred to GREGORY (1910) whose excellent synopsis goes back as far as RAY (1693).

The Insectivores, representing the most primitive order of the Monodelphia, display a marked diversity. Varied adaptations are to be expected from the opportunities afforded by the very great phylogenetic age of the group. But because of the polymorphism of the group, (which never fails to arouse comment) systematists have had great difficulty in finding adequate criteria for

its classification. Up till now the Insectivores were subdivided (HAECKEL 1866) by the presence or absence of the caecum into the suborders Menotyphla and Lipotyphla. This classification was fairly unanimously accepted, but only for convenience since the inadequacy of our embryological, morphological and palaeontological knowledge of the group precluded a natural classification. So we find that WEBER (1928) writes: "Ihre (Insectivora) taxonomische Verteilung in Menotyphla und Lipotyphla, ganz davon abgesehen, dass dabei ein ganz untergeordenetes Merkmal zur Namengebung verwendet wurde, ist eine einigermassen künstliche die nur zum Teil den genetischen, gruppenweisen Zusammenhang zum Ausdruck bringt. Ihre Aufrechthaltung geschicht hier aus praktischen und didaktischen Gründen" (p. 113).

The different aspects of the problematic group have been studied in more recent times by BROOM, LE GROS CLARK, SIMPSON, DE BEER, HENCKEL, JACOBSON, SONNTAG, CARLSSON, VAN DER KLAAUW, GREGORY and others, and various radical changes in the existing taxonomy of the Insectivores have been proposed. These will now be discussed.

The Family Tupaiidae, with its subfamilies Tupaiinae and Ptilocercinae, has perhaps had the most attention. These small arboreal animals of the Orient were first believed to be typical Insectivores, but their remarkable Primate affinities have been revealed by more recent research.

In 1886 PARKER had already noted the resemblance between Tupaiids and the Lemuroidea. Similarly KAUDERN (1910) emphasises the remarkable similarity in the abdominal musculature of the Tupaiidae and the Lemuroidea and concludes: "dass Tupaia und die Halbaffen einer gemeinsamen Wurzel entstammen, die aber freilich einer sehr entfernten Zeit angehört, da sich die madagassischen Halbaffen warscheinlich schon während der ersten Hälfe der Tertiärzeit von den übrigen Halbaffen gesondert haben" (p. 573). GREGORY (1910) also regarded the Tupaiidae as a morphologically annectant form between the true Insectivores and the Lemuroidea, and in 1913 he decided that "even although Tupaiids and Lemuroids may have separated very early, and even although many of the similarities may have developed under the stimulus of similar arboreal habits, yet there is a real generic relationship between the two groups" (pp. 248—249).

The separation of the Tupaiids and Lemuroids took place very long ago since in the Bridger Eocene there existed primitive Tupaiid Insectivores (Entomolestes) and primitive Lemur-like Primates. Although less widely separated than the modern forms they were even then referable to distinct orders.

CARLSSON (1922) recognised that GREGORY's (1910) view was plausible, but she maintained further: "Es scheint mir als ob die Tupaiidae nicht zu den Insectivoren gerechnet werden dürfen, sondern eine eigene Unterordnung der Prosimiae bilden" (p. 268). Using the tongue as a criterion SONNTAG (1925)

VOL 28 194

agreed with the previous authors on the close affinities of the Tupaiidae and the Prosimiae, but he does not altogether exclude the Macroscelidae from these relations, maintaining that the sublingua in the Macroscelidae has become reduced as in Tarsius while in Tupaia it has become specialized as in the Lemuroidea.

LE GROS CLARK, in a series of papers on different aspects of the Tupaiidae, agrees with the above-mentioned authors on the Primate affinities of this group. Discussing the myology of Tupaia he (1924 a) states: "that Tupaia, in its musculature shows very remarkable resemblances to the Prosimiae and corresponding differences from the Lipotyphlous Insectivora. Were a systematist in this case to rely entirely on comparative myology there is little doubt that Tupaia would be approximated to the former and separated from the latter order". He (1924 b) points out that the osteology, myology, vascular and genital systems also show Primate features as does the brain which "indicates that the Tupaiidae may logically be regarded as having attained a status which would justify their inclusion in the Primate Phylum" (p. 1073). In 1925 LE GROS CLARK found further confirmation for the Primate affinities of the Tupaiidae in the skulls of different species, and in 1926 in a monograph on the anatomy of Ptilocercus, he came to the following interesting conclusions: "Broadly speaking it may be said that Ptilocercus and Tupaia represent two successive phases in the evolutionary development of a Lemurid from a primitive insectivorous eutherian mammal. Ptilocercus is a remarkably generalised and primitive arboreal mammal. Tupaia exhibits many differences from Ptilocercus and these differences in almost every case indicate a closer approach to the Lemuroidea. Such conclusions serve to emphasise the truth of the supposition that there is a very real affinity between the Tupaiidae and the Lemuroideae."

SIMPSON (1931 a) prefers to support the classical inclusion of the Tupaioidea with the Insectivora and divides this order into eight super-families. His superfamily, the Tupaioidea (= Menotyphla of HAECKEL), contains three families viz: Anagalidae (SIMPSON 1931 b), Tupaiidae and Macroscelidae. Simpson, however, thinks the Tupaiidae are more closely related to other Insectivores than CARLSSON supposes. He derives the Tupaiidae, Erinaceidae and the Macroscelidae from a common ancestor but maintains that differentiation probably occurred in Palaeocene times. Whether the Macroscelidae arose from the Erinaceus stem after the latter became separated from the Tupaiidae or whether it arose from the Tupaiid stem after separation of the Erinaceidae is according to SIMPSON an open question, depending on one's personal evaluation of the importance and antiquity of the characters.

With SIMPSON, LE GROS KLARK (1932) abandons the distinction of Lipotyphla and Menotyphla, but in addition he places the Tree-Shrews and Elephant-Shrews in separate superfamilies. This is done because "it would be difficult to conceive

two small Mammalian brains which are more fundamentally different and divergent in their structure than those of Macroscelides and Tupaia". On the other hand LE GROS CLARK admits that although Tree-Shrews should logically be classified as primitive Primates as has been suggested by GREGORY, CARLSSON and WOOD JONES (1929), they are still much more primitive than any recent member of that order. Finally LE GROS CLARK (1934) concludes: "The position of the tree-shrews would be more correctly interpreted by finally removing them from their associations with the Insectivora and including them among he Primates of which, no doubt, they represent extremely primitive forms" (p. 251).

Although the evidence for separating the Tupaiidae from the Insectivora seems to be overwhelming, opinions to the contrary have also been expressed. LORENZ (1927) in a paper on the Tupaia hand, and HENCKEL (1928 a and b) both deny all generic relationship between the Tupaiidae and the Primates. Similarly VAN DER KLAAUW (1929) found an entotympanic bone, a proc. tympanicus alisphenoidei and perhaps even a small proc. tympanicus basisphenoidei in the auditory bulla of the Tupaiidae and concludes from this that the Tupaiid bulla is definitely more like that of the Insectivores than that of the Primates.

Whatever their exact systematic position, it is fairly generally accepted that the Tupaiidae represent the closest living relatives of the Primates.

Concerning the affinities of the Macroscelidae, BROOM (1902 b) concludes: "from the fact that Macroscelides agrees with the Marsupials in every detail of this region (i.e. the organ of JACOBSON and anterior paraseptal cartilages) we are forced to the conclusion that it is a very near relative of the Marsupials and has probably very little affinity with the more typical Insectivores" (p. 227).

BROOM (1915 a) inferred from the organ of JACOBSON a close affinity of Tupaia with Macroscelides and the polyprotodont Marsupials while no near relations with Erinaceus and Gymnura could be established. For this reason BROOM (1915 b) advises that "the order Menotyphla to which they (i.e. Macroscelides and Tupaia) belong must be removed far from the Insectivora and placed in quite a different phylum and not far from early Marsupials" (p. 353). GREGORY (1910) also prefers to place the Menotyphla in a distinct order and, with BROOM, ELLIOT, SMITH (1902) and PARKER (1886), recognises certain Marsupial affinities. He establishes a single superorder, the Archonta to embrace the Orders Menotyphla, Dermoptera, Chiroptera and Primates, to emphasize the hypothesis that these orders have had a common origin "possibly from some upper Cretaceous family resembling in many characters the Tupaiidae" (p. 322).

CARLSSON (1909), discussing the affinities of the Macroscelidae, concluded that the suborder Menotyphla was not justified, since its characteristics viz.

VOL
28
194

a long pubic symphysis, an os bullae and a caecum might have evolved by convergence in unrelated groups. Furthermore she stresses the striking differences between the Macroscelidae and the Tupaiidae in the brain, dentition, position of the testes and the relations of the male accessory genital glands. Finally she provisionally linked the Macroscelidae to the Lipotyphlous Erinacidae and thought it reasonable to assume that the Macroscelidae derive from the ancient Erinaceus stock. In 1922 CARLSSON reaffirmed the opinion expressed in her previous work.

In 1928 LE GROS CLARK decided that the cerebral anatomy of the Macroscelidae and Tupaiidae "suggests that the two families represent widely divergent forms", and he maintained that this evidence is quite compatible with CARLSSON's hypothesis (1909) which derives the Macroscelidae from the ancient stock of Erinaceidae. SIMPSON (1931) also accepts CARLSSON's views on the affinities of the Macroscelidae and the Erinaceidae and therefore discards the subdivision of the Insectivores into the Lipotyphla and Menotyphla.

Using the tongue as a criterion SONNTAG (1925) stated that the tongues of the Insectivora represent two radiations corresponding to the Lipotyphla and Menotyphla, the tongues of the Menotyphla being much more primitive than those of the Lipotyphla. Furthermore this author maintained that the Lipotyphla and Menotyphla must have diverged from a common stock. The members of this stock must have possessed all the characters of the primitive Mammalian tongue which are retained among the Mammals only in the Menotyphla and the Primates.

Apart from the Menotyphla the only other group of Insectivores about which much confusion still exists is that of the Golden Moles. By contrast with the Tupaiidae our knowledge of Chrysochlorid embryology is sadly deficient as specimens are particularly hard to get in the breeding season.

BROOM (1916) pointed out that the cranial bones of Chrysochloris fuse early so that in the adult it is impossible to do more than speculate on their structure. He described the skull of a juvenile specimen and drew attention to some remarkable features which, however, were difficult to account for without other embryonic stages. In discussing the results of this investigation and of previous work (1915 a and b) on the organ of JACOBSON in Insectivores, BROOM concludes: "the examination of the skull confirms the result of the examination of Jacobson's organ and its relations, in showing that Chrysochloris is not a near ally to Centetes, and that it is not an Insectivore. Further it is not allied to the Menotyphla and ought to be placed in a distinct order Chrysochloridae" (BROOM 1916, p. 458).

DOBSON (1883) agreed that the Golden Moles and Centetes were naturally related, but emphasised some important differences which indicate their early phylogenetic separation.

SHORTRIDGE (1934) and ROBERTS (1937) have accepted BROOM's views

without any reservations and raise both the Menotyphla and Chrysochloridae to separate orders. On the whole, however, these views of BROOM have not been generally accepted. WEBER (1927, 1928) still maintains the close affinity of the Centetidae and the golden moles, while SIMPSON (1931) merely raises the golden moles to a separate superfamily of the Insectivores.

The remaining groups, viz: Centetidae, Solenodontidae, Erinaceidae, Soricidae and Talpidae form a natural unity and their systematic position as "typical Insectivores" is unquestioned.

Turning to the Insectivore of this research (*Suncus orangiae*) we find that it belongs to the family Soricidae and was first described by ROBERTS (1924) as *Pachyura orangiae*, but CABRERA (1924) pointed out that the generic name *Pachyura* was antidated by *Suncus* so that the latter name has priority. In size *Suncus orangiae* is intermediate between *Suncus varilla* (THOMAS) and *Suncus chryseos* (KERSHAW).

Acknowledgments: To Professor VAN DER HORST of the Department of Zoology, University of the Witwatersrand, Johannesburg I wish to express my sincere thanks for placing the valuable collection of embryonic material in his Department at my disposal. I also wish to express my sincere thanks to the Department of Education for a Government Research Grant which enabled me to collect additional embryonic material.

II. MATERIAL AND TECHNIQUE.

The embryonic material of *Suncus orangiae* was principally collected at Bronkhorstspruit, Eastern Transvaal, and fixed in Bouin solution. The heads of the older embryos and juvenile specimens were decalcified in Ebner's solution. This took from a few days to three weeks. After neutralization and dehydration they were embedded in paraffin wax (m.p. 54° C). Transverse serial sections were cut at a thickness of 10 μ in the younger, and 15 μ in the older embryonic stages.

Before dehydration the material was bulk-stained in Borax Carmine for about three days at 40° C. The sections were counterstained with a solution of Aniline Blue, Orange G and Acetic Acid, with good results.

The following were the crown-rump measurements of the embryos used for this research: 6 mm; 6.8 mm; 7.2 mm; 8.4 mm; 9.5 mm; 15.6 mm; 18.3 mm; 22 mm; 23.5 mm; 28 mm. A further specimen of approximately 6.4 mm was sectioned.

The sections were projected with the "Panphot" microscope and the drawings were reconstructed on graph paper.

A wax model, (100 ×) was made of the nasal region of Suncus (15.6 mm) to help in the interpretation.

III. THE CHONDROCRANIUM.

FAWCETT's (1917) descriptive method will chiefly be followed. This author divided the chondrocranium into the central stem, its appendages, lateral structures, the commissures of the lateral structures and the dorsal structures.

The Suncus chondrocranium reaches its optimal development at about the 15.6 mm stage.

A. THE CENTRAL STEM.

Morphologically the central stem is made up of:

(I) A chordal region which is closely but variously related to the notochord. It is also called the planum basale or the parachordal plate, and usually arises in the early ontogeny of lower vertebrates as paired rods on either side of the notochord. These parachordals may show segmentation not present in Mammals.

(II) The prechordal region of the central stem lies in front of the anterior tip of the notochord, and it presents many problems, particularly in Mammals. In lower Vertebrates this region is formed by the fused trabeculae cranii which usually develop separately on either side of the hypophyseal stalk. The trabeculae may not join the basal plate directly in which case a pair of "polar cartilages", first described by VAN WYHE (1922) becomes interposed. GOODRICH (1930) was still uncertain as to the importance of these elements which might merely represent the hind ends of the trabeculae separately chondrified.

Little is known about the phylogenetic significance of the trabeculae cranii themselves, which might be of visceral or axial origin or might represent entirely new formations. GOODRICH (1930, p. 239) concludes: "On the whole the trabeculae are best considered as structures sui generis developed to support and protect the fore-brain and nasal sacs."

MARINELLI (1936) remains sceptical about a visceral or an axial origin of the trabeculae, and with GOODRICH he concludes "das es sich hier um Bildungen besonderer Art handle" (p. 217).

DE BEER (1931) investigating the early development of the trabeculae in Selachians, Teleosts and Amphibia, supported Huxley's original opinion that the trabeculae cranii were of visceral origin.

In Mammals the base of the prechordal cranium is rather difficult to interpret. It usually arises in two regions:

(i) A median rod extending from the hypophysis to the region between the nasal cavities. It is called the Pars Interorbitonasalis by FAWCETT, the anterior trabecular element by GOODRICH, and the trabecular plate by STADTMÜLLER. The last will be used in this paper.

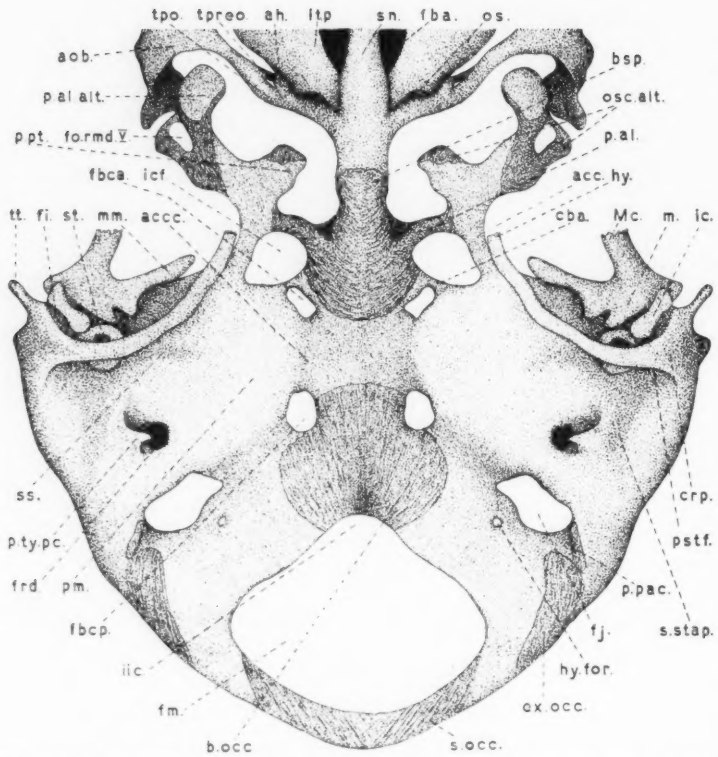

Fig. 1. Ventral view reconstruction of the sphenoidal and auditory regions of the chondrocranium of a 15.6 mm embryo—indicating the position of ossification centres present at that stage (× 20).

(ii) Paired cartilages, one on either side of the hypophyseal stalk, but medial to the internal carotid arteries.

Later on these elements fuse with one another thus closing up the fenestra hypophyseos. They also fuse with the basal plate behind and with the trabecular plate in front. This region is called the Pars Trabecularis by FAWCETT. It is also named Lamina Hypophyseos by other authors. Because of the doubt which exists about the homology of this structure, the author prefers to use the non-committal term "lamina hypophyseos" which merely expresses its anatomical relations.

At the stage of optimal chondrification of the primordial cranium in Suncus the parts of the central stem are in direct continuity. There is no demarcation of their union, but it is not difficult, even at this stage, to gauge their limits with moderate precision from surrounding landmarks.

The *planum basale* (figs. 1 and 2) is roughly triangular in shape. The base of the triangle forms the concave border of the incisura intercondyloidea and, laterally, with the Hypoglossal foramina as landmarks, it merges into the pila

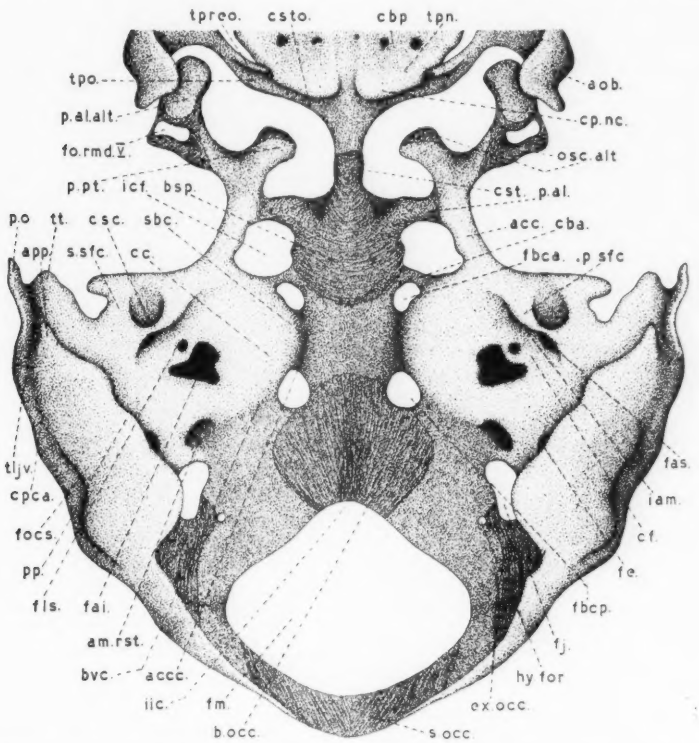

Fig. 2. Dorsal view reconstruction of the sphenoidal and auditory regions of the chondrocranium of a 15.6 mm embryo—indicating the position of ossification centres present at that stage (× 20).

occipitalia. This basal region of the triangular plate is very thin especially along the mid-line in front of the foramen magnum. It is slightly concave above forming a shallow fossa medullae oblongatae. The anterior or apical portion of the basal plate is fairly wide and is separated from the cochlear capsule by the extensive jugular foramen and the basicochlear fissure. It is, however, synchondrotically continuous with the capsule through a wide commissure referred to as the chordo-cochlear commissure by FAWCETT (1917) and basi-vestibular commissure by DE BEER (1937). This commissure is situated between the jugular foramen and basicochlear fissure. A further commissure is present in Suncus which connects the basal plate to the anteromedial aspect of the cochlear capsule. It cuts transversely across the basicochlear fissure and will be referred to as the anterior chordo-cochlear commissure.

DE BEER (1937, plate 115) illustrates a 14 mm stage of Talpa (after NOORDENBOS) which shows a similar arrangement. He mentions, however, that the posterior basicochlear fissure soon becomes obliterated producing a

very wide connection between the basal plate and the cochlear capsule. (See DE BEER 1937, plate 116, figs. 3 and 4, reprinted after FISCHER). LEIMGRUBER (1939, figs. 3 and 4) models the chondrocranium of a 23.5 mm embryo of Centetes which shows a similarly subdivided basicochlear fissure.

Compared with the basal portion of the planum basale the medial and apical portions are much thicker. They show a marked dorsal convexity which slopes steeply downwards on either side to the basicochlear fissure and the deep basicochlear sulcus connecting the two subdivisions of the fissure. Ventrally the anterior part of the planum basale is flat but for slight concavities in places. There is no trace of the chorda dorsalis at this stage.

The *lamina hypophyseos:* (figs. 1 and 2). The posterior end of the lamina hypophyseos, which lies medial to the carotid foramina, is about as wide as the anterior end of the basal plate with which it is fused. This posterior end of the lamina hypophyseos is flat, and on its dorsal surface there is no indication of either a dorsum sellae or a crista transversa. Consequently the fossa hypophyseos is barely visible, as in Sorex (DE BEER 1929). This author (p. 443) gives a list of other Mammals in which a similar condition occurs. Posterolaterally the lamina hypophyseos is attached to the antero-medial aspect of the cochlear capsule by the commissura basicochlearis anterior (posterior trabeculo-cochlear commissure of FAWCETT). Leading from the extreme antero-lateral border of the lamina hypophyseos is the processus alaris which communicates laterally with the alicochlear commissure, and with the basal end of the ala temporalis, the latter connection being secondary.

The *trabecular* plate is a narrow rod, triangular or circular in cross-section. Anterior to the attachment of the optic roots of the alae orbitales and medial to the two orbito-nasal fissures it increases rapidly in dorso-ventral thickness on entering the intranarial region as the septum nasi. This part of the trabecular plate will be described in detail with the nasal capsule.

1. Foramina in central stem: At the optimal stage of chondrification the fenestra hypophyseos (fen. basicranialis ant.) and the fenestra basicranialis posterior are both absent in Suncus.

The carotid foramina are placed on either side of the midline in the mid-transverse plane of the lamina hypophyseos. Each foramen is bounded as follows: posteriorly by the commissura basicochlearis anterior and the anterior aspect of the cochlear capsule; laterally by the alicochlear commissure (representing the hindmost part of the trabecula of lower Vertebrates—DE BEER, also called the anterior trabeculo-cochlear commissure—FAWCETT (1917)) and anteriorly by the processus alaris of the lamina hypophyseos (figs. 1, 2 and 11).

2. Early development of the central stem: It is difficult to distinguish the different parts of the central stem in Suncus, since even in very early procartilaginous stages they form one continuous structure. The

VOL
28
194

trabecular plate is still separate in the 6 mm embryo, but even this blasteme rudiment soon coalesces with the rest of the central stem. Up to the 6.8 mm stage the major part of the central stem remains blastematous—only the basal end of the planum basale being chondrified. At the 7.2 mm stage most of the central stem is chondrified with no visible separation between the regions.

The planum basale shows no indication of either a fenestra basicranialis posterior or paired parachordals at any stage of its development. Even before chondrification the blastematous basal plate is confluent with the blastematous otic capsule with no basicapsular fissure between them. In the 7.2 mm stage practically the entire basal plate is chondrified. The last portion of this region to become chondrified is the connection with the otic capsule, which even at this stage, is very thin and in parts still procartilaginous. In the 8.4 mm stage the connection between the basal plate and the otic capsule is entirely cartilaginous and there is no trace of a basicochlear fissure, neither does the 9.5 mm embryo show this fissure. In the 15.6 mm embryo already described, however, the basal plate is separated from the otic capsule by a subdivided basicochlear fissure.

The relations of the notochord to the basal plate in Suncus are very constant throughout development. The notochord is visible in the 6 mm stage behind the hypophysis and dorsal to the blasteme of the central stem. It remains dorsal to the basal plate until its final resorption in later development. At no stage does the notochord reach beyond the posterior border of the hypophysis. Resorption of the notochord takes place from its anterior end. In the 7.2 mm embryo it still reaches the hypophysis, but in the 8.4 mm stage the anterior part has been resorbed completely and only the posterior end lying dorsal to the basal portion of the planum basale, is present. The notochord is continued posteriorly into the centre of the odontoid process of the axis. In the 9.5 mm embryo it has disappeared altogether but for a short stump between the odontoid peg and the posterior margin of the planum basale.

The reader is referred to STADTMÜLLER's (1936, p. 855) excellent summary of the comparative relations of the notochord to the basal plate.

Since the whole basal plate chondrifies hypochordally in Suncus its notochord is of the retrobasilar type, i.e. according to TOURNEUX's (1912) classification of the notochord types—(quoted after STADTMÜLLER). According to MATTHES (1923) the retrobasilar type of notochord is the most primitive, and it is found in *Mus musculus, Mus rattus* and Xerus (FAWCETT (1923) as well as Echidna (GAUPP 1908) and Ornithorhynchus (DE BEER and FELL 1936).

The lamina hypophyseos remains pro-cartilaginous up to the 6.8 mm stage. It is already chondrified and in cartilaginous continuity with the basal plate in the 7.2 mm stage. Its two constituent elements, the two polar cartilages (or trabeculae of some authors), are separated across the midline even while blastematous.

The fenestra hypophyseos is most extensive in the 7.2 mm embryo (fig. 11). After this stage it gradually becomes smaller as the chondrification of the lamina spreads medially. In the 15.6 mm embryo the foramen is obliterated. The internal carotid arteries enter the cranial cavity lateral to the median lamina hypophyseos. Only in the 8.4 mm embryo do the alicochlear commissures become completely chondrified so as to enclose the internal carotid arteries laterally.

The blasteme rudiments of the ala temporalis and alicochlear commissures are confluent with one another and with the lamina hypophyseos but, as will be described in detail later on, the ala temporalis chondrifies from an antero-lateral autogenous centre, while the chondrification of the processus alaris, which has already begun in the 7.2 mm embryo, spreads outwards from the lamina hypophyseos.

When the chondrification of the processus alaris reaches the attachment of the alicochlear commissure, this commissure chondrifies in continuity with it and not from a separate centre.

DE BEER (1926 and 1928) maintained that the internal carotids of Mammals are not extratrabecular as one might suppose. The internal carotids in Mammals enter the skull on either side of the median cartilage. This cartilage gives off the basitrabecular process immediately in front of the artery. The internal carotid artery is only enclosed laterally when the alicochlear commissure develops. This commissure which lies ventral to the trigeminal nerve and medial to the palatine nerve represents, according to DE BEER, the retarded posterior portion of the trabecula (or polar cartilage).

Since the processus alaris (proc. basitrabecularis) is part of the basitrabecular plate and represents an outgrowth from the trabecula present even in lower Vertebrates, there can be no doubt that the median cartilage (mentioned by DE BEER) which arises as two elements lateral to the cranio-pharyngeal canal, represents the divergent posterior ends of the primitive trabeculae cranii. Even if these elements condrify from separate centres to form the polar cartilages, they probably represent the detached posterior ends of the trabeculae. This has already been suggested by GOODRICH and others. The internal carotid arteries of the Mammalian primordial cranium are therefore partly extra-trabecular. Partly, because the alicochlear commissure, which chondrifies in continuity with the lamina hypophyseos, in all probability represents a retarded outgrowth of the postero-lateral margin of the trabecula and may even fail to develop in some Mammals.

These concepts remind one of GAUPP's theory (1902) that the Mammalian internal carotids have cut through the trabeculae. In Ornithorhynchus (DE BEER 1926) and Echidna (GAUPP 1908) the internal carotids are intratrabecular, this being the primitive condition. Those Mammals with a persistent alicochlear commissure represent an intermediate stage. Ultimately the internal carotids are

VOL
28
194

entirely extratrabecular (ontogenetic development of Primates and adult condition in the majority of Mammals). STADTMÜLLER (1936) appears to accept this interpretation.

The trabecular plate in Suncus arises as a continuous cylindrical rod except for the intranarial portion which has the form of a vertical plate. It merges posteriorly with the anterior end of the lamina hypophyseos. The development of this region, and of the nasal septum in particular, will be dealt with later.

3. Post optimal changes in the central stem: Usually the central stem ossifies from four centres. The most posterior centre occurs in the planum basale and forms the basioccipital, while the centre in the lamina hypophyseos forms the basisphenoid. In the anterior trabecular plate there are usually two ossification centres. The more posterior is usually paired and is situated medial and anterior to the attachment of the alae orbitales. It forms the presphenoid. The other centre which is absent in some Mammals (BROOM) occurs in the intranasal portion of the trabecular plate near the middle of the upper half of the combined cribriform plates; it forms the mesethmoid. The latter centre appears fairly late in the intra-uterine development of Suncus, but once it is formed it expands rapidly backwards and partly replaces the presphenoid. The mesethmoid will be discussed in detail with the nasal capsule.

The presphenoidal region of the central stem was found to ossify in continuity with the orbitosphenoids with which it will be discussed.

Unlike the mesethmoid the basisphenoid in Suncus develops very early. In the 15.6 mm embryo the basisphenoid is fairly extensive, although only perichondrally ossified (figs. 1 and 2). The ossification spreads laterally from a point medial to the carotid foramina into the alar process and the anterior tip of the alicochlear commissure. The middle part of the alicochlear commissure is entirely resorbed by the end of the intra-uterine life, while its posterior end ossifies in continuity with the otic capsule. The carotid foramen (for. lacerum medium) in the adult skull is not enclosed in the basisphenoid as in the Monotremes and Marsupials, but lies lateral to the basisphenoid and is bordered postero-laterally by the petrosum. Since the anterior basicochlear commissure is resorbed in the 22 mm embryo the anterior division of the fissura basicapsularis becomes confluent with the carotid foramen which transmits a small emissary vein as well as the internal carotid artery.

The basisphenoid does not fuse with the alisphenoid till shortly after birth.

Enclosed between the basisphenoid, pterygoid and alisphenoid is the small canalis Vidianus (canalis pterygoideus) which transmits the vidian nerve and a large vein. The basisphenoid does not fuse with the pterygoid, but these elements are separated by a closely knit suture. The posterior part of the basisphenoid which joins the basioccipital is thick and markedly pneumatic. Dorsally it is convex and shows no sella turcica for the hypophysis, which lies over the posterior end of the basisphenoid and the junction between it and the basi-

occipital. Medial to the carotid foramina and for some distance anterior to them, the dorsal surface of the basisphenoid exhibits a wide and shallow concavity. The mid-ventral aspect of this region is deply grooved so that the basisphenoid is rather thin though compact in the midline, while the markedly pneumatic lateral portions are considerably thicker. Medial to the alar process the basisphenoid is perforated by an unpaired median foramen which, however, does not transmit either bloodvessel or nerve. The central portion of the basisphenoid forms the medial and dorso-medial walls of the anterior part of the middle ear.

The basioccipital appears before the basisphenoid. In the 9.5 mm embryo the first trace of a single basioccipital ossification centre is visible very near the apex of the incisura intercondyloidea. This ossification rapidly spreads forwards and laterally. In the juvenile Suncus of 28 mm a narrow strip of slightly perichondrally ossified cartilage still persists between the basioccipital and basisphenoid. At this stage the occipital condyle is also still cartilaginous between its basioccipital and exoccipital components. The anteroventral portion of the occipital condyle is formed by the basioccipital while the exoccipital forms its major postero-dorsal part. Anterior to the jugular foramen, in the region of the commissura basicapsularis posterior, the basioccipital forms an intimate suture with the periotic. Further forward, however, in the region of the posterior division of the basicapsular fissure, an appreciable space intervenes between the lateral edge of the basioccipital and the otic capsule. The fossa medullae oblongatae and fossa pontis could not be clearly distinguished on the upper surface of the basioccipital bone.

B. LATERAL STRUCTURES APPENDED TO THE CENTRAL STEM.

These include: The exoccipital cartilages or pilae occipitales, the auditory capsules, the alae temporales, the alae orbitales with their pre- and postoptic roots and the tectum, paries and solum nasi. The foramina which lie between these structures and the central stem will be discussed with the structure concerned.

1. The exoccipital cartilages are attached to the postero-lateral corners or basal angles of the triangular planum basale of the central stem. There is no separation between the exoccipital cartilage and the central stem but the junction is indicated by the hypoglossal foramen which is single on each side. The medial border of the exoccipital cartilage forms the lateral edge of the foramen magnum and it carries the greater part of the occipital condyle. Antero-ventrally the lamina alaris of the exoccipital is fused to the ventro-lateral aspect of the pars canalicularis behind the jugular foramen. The lateral aspect of the line of fusion between the lamina alaris and the auditory

VOL.
28
194

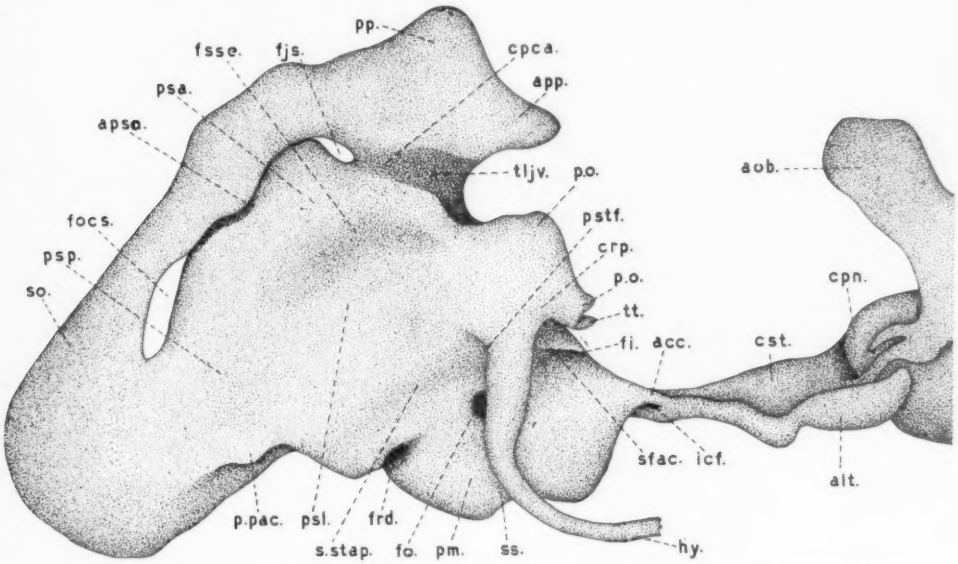

Fig. 3. Lateral view reconstruction of the sphenoidal and auditory regions of the chondrocranium of a 15.6 mm embryo (× 30).

capsule, known as the processus paracondyloideus, is prominent (figs. 1 and 3). The musculus rectus capitis lateralis inserts into it. Viewed from the cavum cranii the recessus supra-alaris (recessus jugularis—FAWCETT), is very wide. It lodges the terminal part of the lateral sinus and, leading from the jugular foramen antero-ventrally it separates the pars canalicularis from the bulk of the exoccipital. Postero-dorsal to the recessus supra-alaria the anterior edge of the exoccipital cartilage (commissura occipito capsularis posterior) is fused to the posterior wall of the pars canalicularis. The fissura occipito capsularis inferior is obliterated in Suncus, as in Sorex (DE BEER 1929) (figs. 3 and 5).

a. *Early development of exoccipital cartilages:* The blasteme rudiments of the pilae occipitales in Suncus were found to be continuous with the basal angles of the blastematous planum basale as early as in the 6 mm embryo. In the 6.8 mm embryo the basal portion of the planum basale was found to be chondrified and in synchondrotic continuity with the exoccipitals. The chondrification of these parts apparently spreads from a single centre in the basal plate so that the exoccipital cartilages are not ontogenetically separate from the basal plate. In both the 6.8 mm and 7.2 mm stages the exoccipital is fairly extensively chondrified. It lacks a cartilaginous lamina alaris so that at these stages the otic capsule and exoccipital cartilage are not in synchondrotic continuity. In the 8.4 mm embryo the lower end of the lamina alaris has already come into cartilaginous continuity with the otic capsule, but its postero-dorsal end is still procartilaginous so that the fissura occipito-capsularis extends very

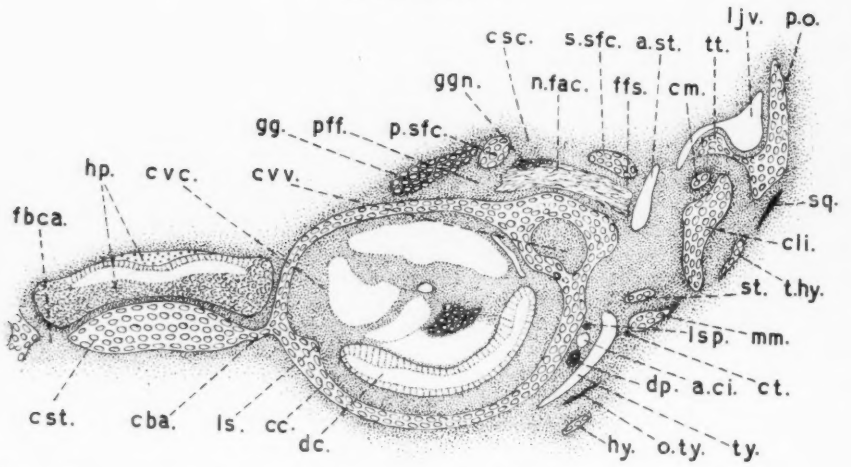

Fig. 4. Transverse section of the front portion of the cochlear capsule of a 15.6 mm embryo (× 35).

far downwards. Chondrification in the lamina alaris spreads from its antero-ventral to its postero-dorsal end and in the 9.5 mm embryo the optimal stage of chondrification is practically reached. The supra- and exoccipitals have already fused in the 8.4 mm embryo.

b. *Post optimal changes in exoccipital cartilages:* The first signs of ossification in the exoccipital cartilages of Suncus were observed in the 15.6 mm embryo, where fairly extensive perichondral ossification had set in (figs. 1 and 2). The exoccipitals do not fuse with the supraoccipital until shortly after birth. Ventrally the exoccipital forms the major postero-dorsal part of the occipital condyle. The alar ligament leads from the antero-ventral tip of the odontoid process and attaches to the ventro-medial edge of the exoccipital just postero-dorsal to its junction with the basioccipital. The hypoglossal canal pierces the extreme basal end of the exoccipital. The latter structure also forms the posterior and postero-medial borders of the jugular foramen. The processus paracondyloideus of the exoccipital cartilage appears to ossify from a separate centre which, however, remains separate only for a very brief period and becomes confluent at a very early stage with the rest of the exoccipital bone. In the skull this process is known by a variety of names, e.g. Proc. paramastoideus, paroccipitalis, retromastoideus, basilaris, jugularis, paracondyloideus.

2. In the auditory capsule of Suncus (figs. 1, 2, 3 and 5) two main parts are readily distinguished, viz: the pars canalicularis or pars posterior (which is postero-dorsal in position and lodges the semicircular canals and utricle), and the pars cochlearis or pars anterior (which lies antero-ventrally and lodges the saccule and ductus cochlearis). The pars cochlearis converges towards its fellow anteriorly thus confining the planum basale of the central stem to an area far narrower in front than behind.

VOL 28 194

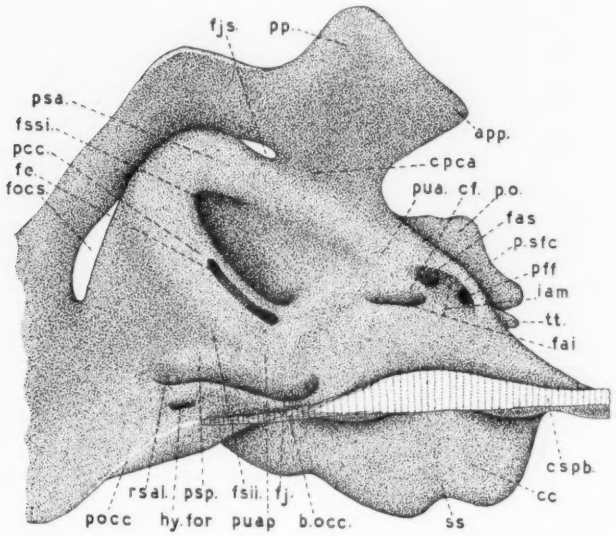

Fig. 5. Medial view reconstruction of the auditory capsule of a 15.6 mm embryo (× 30).

Some of the connections of the auditory capsule to neighbouring parts of the chondrocranium have already been discussed. Thus the pars cochlearis is attached to the lamina hypophyseos by: (a) the alicochlear commissure (anterior trabeculo-cochlear commissure of FAWCETT) and (b) by the anterior basicochlear commissure (posterior trabeculo-cochlear commissure of FAWCETT). To the planum basale it is attached by the commissura basicochlearis posterior (chordo-cochlear commissure of FAWCETT), as well as by a narrow anterior chordo-cochlear commissure.

The pars canalicularis is connected to the antero-ventral edge of the exoccipital through the joined lamina alaris and commissura occipito-capsularis posterior.

Antero-dorsally the pars canalicularis gives rise to the anterior capsulo-parietal commissure which connects it to the lamina parietalis. The lamina parietalis lies in a vertical plane with a slight dorso-medial inclination. It is roughly quadrilateral in shape. Anteriorly it is free since the orbito-parietal commissure is deficient. Posteriorly the parietal plate is connected to the supraoccipital through the occipito-parietal commissure. A well defined fissura occipito-capsularis superior (anterior) (v. fissura parieto-capsularis) is enclosed between the ventral margins of the parietal plate and supraoccipital and the dorsal margin of the pars canalicularis, posterior to the attachment of the commissura parieto-capsularis anterior and anterior to the commissura occipito-capsularis posterior. The anterior end of this fissure transmits the lateral jugular vein and it is commonly referred to as the foramen jugulare spurium.

The lateral jugular vein after emerging from the foramen jugulare spurium runs in a deep trough lateral to the commissura capsulo-parietalis anterior. It then descends over the anterior surface of the cochlear capsule.

The tegmen tympani springs from the antero-lateral border of the pars canalicularis and projects forwards for a short distance over the fossa incudis. Its root contributes to the formation of the roof of the sulcus facialis, and postero-laterally it fuses with the crista parotica (crista facialis of VAN DER KLAAUW) which forms the lateral wall of the sulcus facialis. The ventral border of the crista parotica is continuous with the upper end of the hyoid arch (tympano-hyale) which projects downwards, inwards and forwards. The posterior border of the root of the tympano-hyale forms the outer anterior margin of the primary stylomastoid foramen through which the main part of the facial nerve emerges. A mastoid process on the otic capsule is absent or very inconspicuous. The processus opercularis is exceptionally large in Suncus (figs. 3 and 5) and its relations are not markedly different from those found in Sorex (DE BEER 1929) and Talpa (FISCHER 1901). It is a broad vertical plate which lies in a plane lateral to the otic capsule. Antero-ventrally the opercular process merges into the crista parotica. They lie in the same plane and together display a smooth slightly convex outer surface. Ventro-medially the opercular process is attached to the lateral baseline of the tegmen tympani (fig. 6) and to the anterior dorso-lateral aspect of the pars canalicularis. The anterior and dorsal edges of the processus opercularis are free. The anterior edge projects as far forward as the tegmen tympani does. The upper edge of the opercular process forms the ventro-lateral border of the deep trough in the lateral aspect of the commissura parieto-capsularis anterior. This trough lodges the lateral jugular vein as it runs downwards and forwards from the foramen jugulare spurium. It also lodges the arteria meningia media which runs upwards and backwards from the arteria stapedialis. FAWCETT (1917, p. 320) describes an anterior prolongation of the supraoccipital cartilage which overlaps the pars canalicularis above as far as the most prominent part of the prominentia subarcuata superior and calls it a "processus opercularis". In 1919 he reported a similar "opercular process" in Miniopterus. DE BEER (1929) approves of FAWCETT's use of this name and recognises the possibility of the homology suggested by FAWCETT. Actually he regards the homology as quite probable based on an examination of the attachment of certain pectoral muscles, and from the peculiar position of the processus opercularis in Sorex and Talpa which suggests a secondary shift into that position. DE BEER concludes, therefore, that the condition in Microtus (FAWCETT 1917) is probably the more primitive, the difference in the degree of fusion of the opercular process with the neighbouring cartilaginous structures being probably associated with function. Apart from the opercular process described for Suncus, however, it was found that the supraoccipital also bears a slight

VOL
28
194

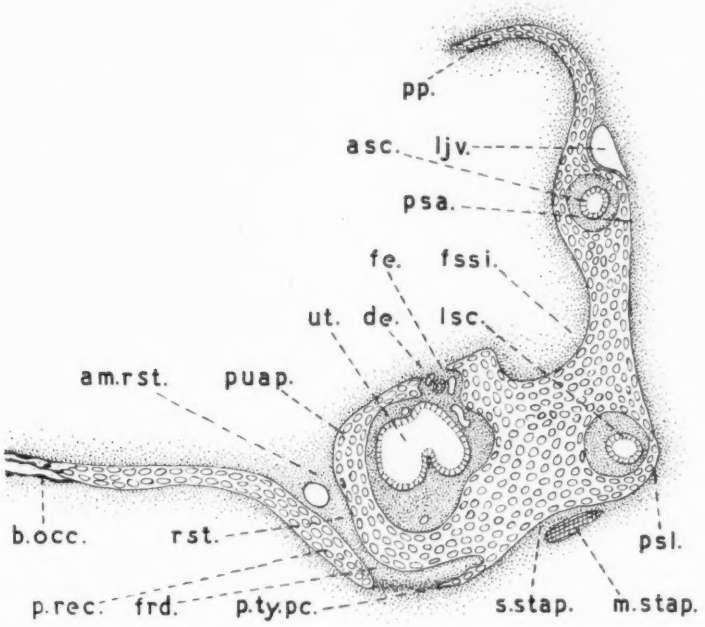

Fig. 6. Transverse section through the pars canalicularis of the auditory capsule of a 15.6 mm embryo (× 40).

anterior prolongation which overlaps the pars canalicularis postero-dorsally, thus concealing the middle portion of the fissura occipito-capsularis superior (fig. 3). This prolongation, though less conspicuous, corresponds exactly in position to the so called "processus opercularis" of Microtus and Miniopterus. The structures concerned are undoubtedly homologous. If DE BEER'S theory on the origin of the processus opercularis of Sorex and Talpa is correct, then this structure in Suncus would represent a detached terminal portion of the anterior prolongation of the supraoccipital which became secondarily fused to the otic capsule in the position already described. Thus Suncus would represent an interesting intermediate stage. This question, however, cannot be solved without studying developmental evidence, and will therefore be discussed later.

The pars canalicularis of the otic capsule is roughly triangular with the apex directed obliquely backwards and upwards. on its medial surface the pars canalicularis is deeply indented by the fossa subarcuata superior (anterior) interna (fig. 5). This fossa is bound dorsally and postero-dorsally by the prominentia semicircularis anterior. Antero-dorsally the fossa subarcuata superior interna is bound by the prominentia utriculo-ampullaris anterior (superior). The posterior crus of the suprafacial commissure rests on this eminence and arches forwards and inwards to the antero-dorsal aspect of the

cochlear capsule to enclose the primary facial foramen. From this foramen the facial nerve enters the cavum supracochleare or hiatus spurius. Here the greater superficial petrosal or palatine nerve runs forward while the rest of the facial nerve is continued through the foramen faciale secundarium into the sulcus facialis. The bridge over the secondary facial foramen springs from the antero-dorsal aspect of the pars canalicularis and arches to the antero-lateral side of the pars cochlearis. Postero-ventrally and ventro-medially the fossa subarcuata superior interna is bound by the prominentia cruris communis containing the crus commune of the anterior and posterior semicircular canals, while more antero-ventrally it is bound by the prominentia utriculo-ampullaris posterior inferior with its sinus superior. The base of the medial surface of the pars canalicularis would therefore, be represented by an imaginary oblique line drawn through the prominentia utriculo-ampullaris superior and inferior.

The infero-medial surface of the pars canalicularis is mainly directed towards the lamina alaris of the exoccipital. Dorsally it is bordered and roofed over by the prominentia cruris communis. The whole infero-medial surface is concave and it has at its base a slight prominence postero-dorsal to the jugular foramen which corresponds to the inconspicuous prominentia semicircularis posterior and the prominentia utriculo-ampullaris posterior. The recess dorsal to these prominences is the shallow fossa subarcuata inferior (posterior) interna and ventral to it lies the recessus supra-alaris. These two recessus, however, are not clearly demarcated and merge into one another posteriorly where the prominentia semicircularis posterior disappears.

The lateral surface of the pars canalicularis (fig. 3) is quadrilateral in shape being bordered anteriorly by the prominentia utriculo-ampularis anterior, superiorly by the prominentia semicircularis superior (anterior), posteriorly by the prominentia semicircularis posterior and ventrally by the prominentia semicircularis lateralis. Between these prominences the lateral surface of the pars canalicularis shows a slight concavity, known as the fossa subarcuata superior externa. The cartilaginous base of this fossa may, however, be convex laterally and not concave, in which case it is referred to as the prominentia subarcuata superior externa.

The pars cochlearis may be divided for convenience into a cochlear and a vestibular segment which contain respectively the cochlear duct and the saccule. The vestibular portion of the pars cochlearis is wedged in between the pars canalicularis and the cochlear segment of the pars cochlearis. Laterally there is no demarcation between the cochlear and vestibular portions of the pars cochlearis but the sulcus facialis and its posterior continuation, the sulcus musculi stapedii, delimit the vestibular segment from the pars canalicularis. Medially there is hardly any recognisable demarcation between the segments of the pars cochlearis. The foramina in the vestibular segment will be discussed later.

VOL
28
194

The cochlear segment is dome-shaped and is directed forwards and medialwards. The cochlear segments, however, are rather small and do not constrict the anterior portion of the planum basale to any great extent. The rounded anterior end or cupula anterior ends postero-lateral to the carotid foramen. The dorsal surface of the cochlear segment is smooth, slightly convex and not indented by any sulci (fig. 2). The ventral surface projects far below the central stem (fig. 3) and is more markedly convex than the dorsal surface. Ventral to the fenestra ovale and directly medial to Reichert's cartilage the ventro-lateral wall of the pars cochlearis shows a deep vertical sulcus (figs. 1 and 3) the upper part of which is occupied by the stapedial artery and the lower part by the internal carotid before the stapedial artery branches off. Having given off the stapedial artery the internal carotid runs forwards and upwards round the anterior face of the stapes and courses medial to the incus and malleus. In the fossa incudis the internal carotid runs ventro-medial to the tensor tympani muscle and lateral to the cupula anterior of the pars cochlearis. It is continued forward over the anterior face of the cochlear capsule and enters the cranial cavity through the carotid foramen. The stapedial artery pierces the stapes and gives off the arteria meningia media which runs upwards and backwards for some distance with the lateral jugular vein. The rest of the stapedial artery runs forwards in the fossa incudis but dorsolateral to the tensor tympani muscle. Having emerged from the fossa incudis the stapedial artery follows the medial border of Meckel's cartilage for some distance. The medial surface of the cochlear segment is attached to the central stem by the commissures already described.

a. *Foramina in the wall of the auditory capsule:* Postero-medial to the suprafacial commissure a depression in the medial wall of the vestibular segment, known as the internal auditory meatus, leads to several important foramina (fig. 2). Its anterior end leads to the primary facial foramen bridged over by the suprafacial commissure. The posterior portion of the meatus is divided by the crista falciformis into; I. a dorsal division, or foramen acusticum superius, which transmits branches of the auditory nerve to the utricle, the ampullae of the anterior and lateral semicircular canals, and the dorsal and posterior divisions of the saccule, and II. a much larger ventral division or foramen acusticum inferius. This foramen transmits the lower nerve to the saccule, the cochlear nerve and a small nerve to the ampulla of the posterior semicircular canal. The cochlear nerve in Suncus is enclosed in a separate foramen as in Microtus (FAWCETT 1917) but a separate "foramen singulare" for the nerve of the posterior canal is not isolated.

The foramen endolymphaticum for the ductus endolymphaticus is rather complicated (fig. 5). The ductus endolymphaticus runs along the dorso-medial aspect of the crus commune of the posterior and anterior semicircular canals. Immediately behind the prominentia utriculo-ampullaris posterior (inferior)

the ductus endolymphaticus breaks through the dorso-medial cartilaginous wall of the prominentia cruris communis and runs backwards for a short distance in a shallow groove along the dorso-medial aspect of the latter prominence. The ductus endolymphaticus again enters the cavity containing the crus commune and is then continued backwards to the extreme postero-dorsal end of the cavity where it passes through a small foramen in the cupula posterior of the pars canalicularis (not visible from the medial side) and immediately dilates into the saccus endolymphaticus medial to the supra-occipital.

The aqueductus cochlea: The posterior end of the cochlear segment of the pars cochlearis becomes the cavum perilymphaticum and the recessus scalae tympani. The floor of this recess is formed by the processus recessus which actually represents a posterior continuation of the ventral wall of the pars cochlearis. The roof of the recess and of the aqueductus cochleae is formed by the floor of the posterior end of the pars canalicularis which ends anteriorly as a free shelf. The anterior border of this shelf forms the posterior border of the foramen perilymphaticum. Medially the processus recessus is confluent with the lateral border of the planum basale and immediately dorsal to this confluence the medial wall of the recessus scalae tympani is deficient forming the apertura medialis through which the ductus perilymphaticum enters the cranial cavity. Posteriorly the processus is again confluent with the floor of the pars canalicularis. Similarly the lateral border of the planum basale joins the ventro-medial wall of the pars canalicularis for a short distance before it separates again at the foramen jugulare.

The fenestra rotunda is an oval aperture in the postero-lateral aspect of the wall of the pars cochlearis. It faces downwards, outwards and backwards. Its anterior boundary is formed by the posterior edge of the vestibular segment of the pars cochlearis. Ventro-medially it is bound by the lateral edge of the processus recessus, dorsolaterally by the ventro-lateral wall of the prominentia utriculoampullaris posterior (inferior), while posteriorly the fenestra rotunda is bound by the floor of the prominentia utriculo-ampullaris posterior and the postero-lateral border of the processus recessus fused to it. The fenestra rotunda is situated at the base of a short but deep lateral sulcus which runs parallel but ventral to the sulcus musculi stapedii. This short sulcus lodges the postero-ventral extremity of the middle ear and is partly covered over by a thin plate of cartilage which projects like a lid from the lateral side and springs from the ventral border of the sulcus musculi stapedii (fig. 6). Posteriorly this cartilaginous lid which partly hides the fenestra rotunda and the posterior tip of the middle ear is fused to the ventral aspect of the prominentia utriculo-ampullaris and to the lateral edge of the processus recessus. This cartilaginous lid undoubtedly represents a small caudal petrosal tympanic plate which is in direct continuity with the otic capsule. The antero-medial and ventro-medial edges of this tympanic plate are free. These edges, however, are in very strong

VOL.
28
194

syndesmotic continuity with the otic capsule ventro-medial to the fenestra rotunda.

The fenestra ovalis (fenestra vestibuli) in the lateral wall of the vestibular segment of the pars cochlearis lodges the foot of the stapes and it faces the sulcus facialis opposite the root of the tympanohyale.

b. *The interior of the auditory capsule:* As VOIT (1909) pointed out in the rabbit, the external form of the auditory capsule is intimately dependant on the form of the membranous labyrinth. The latter is contained in a complicated system of interconnecting spaces which, like the cartilaginous auditory capsule, can be divided into cochlear and canalicular portions, and the former can again be subdivided into a vestibular and a cochlear segment. These parts do not differ greatly from the general Mammalian type, therefore the description will be brief.

OL.
28
947

The cavum vestibulare lies between the cavum cochleare and the cavum canaliculare. It lodges the saccule, the canalis reuniens and the proximal portion of the ductus cochlearis. Ventro-medially it is directly continuous with the cavum cochleare, the posterior portion of which becomes the cavum perilymphaticum and the recessus scala tympani. Only the extreme anterior end of the cavum vestibulare is completely separated from the cavum cochleare by the basal portion of the septum spirale. This portion of the septum spirale is attached to the ventral aspect of the anterior part of the crista falciformis and separates the first turn of the ductus cochlearis and the saccule from the second turn of the cochlear duct. The apical portion of the septum spirale is attached to the floor of the cavum cochleare anteriorly, it is poorly developed in Suncus and its attachment to the cochlear capsule is not visible from the outside as a sulcus septalis. The cavum canaliculare contains the utricle, the semicircular canals with their ampullae and the crus commune of the anterior and posterior semicircular canals. The anterior part of the cavum canaliculare containing the utricle and the expanded portion which forms the recessus utriculo-ampullaris anterior and lateralis communicates freely with the cavum vestibulare. The posterior portion of the cavum canaliculare however, has a well-defined floor which projects forwards as a shelf over the cavum perilymphaticum and the aqueductus cochleae. The anterior border of this shelf has been mentioned before as forming the posterior border of the foramen perilymphaticum. Its medial border is continued forwards for some distance as a prominent ridge on the ventro-lateral aspect of the dorso-medial wall of the pars cochlearis. The ridge forms part of the boundary between the cavum vestibulare and the cavum cochleare. It leads as far forwards as the crista falciformis and, although quite inconspicuous in this region, it seems to be confluent with the septum spirale. The small branch of the auditory nerve leading to the ampulla of the posterior semicircular canal and, which in Suncus is not enclosed in a foramen or canalis singulare, runs backwards immediately

lateral to this ridge. The posterior part of the cavum canaliculare expands into the recessus utriculo-ampullaris posterior (inferior) which receives the posterior opening of the lateral semicircular canal and the lower ampullate opening of the posterior semicircular canal. Just anterior to the recessus utriculo-ampullaris posterior the cavum canaliculare gives off the sinus superior through which the crus commune of the anterior and posterior semicircular canals communicate with the utricle.

c. *Early development of the auditory capsule.* The first part of the auditory capsule to chondrify is the pars canalicularis. Even in the 6.8 mm embryo where the major part of the otic capsule is still procartilaginous the cupula posterior and massa angularis of the pars canalicularis shows signs of slight chondrification. In the 7.2 mm embryo the greater part of the otic capsule is chondrified. The following parts, however, are still procartilaginous: The roof of the pars cochlearis, the crista falciformis, the lamina spiralis, the floor, roof and medial wall of the cavum perilymphaticum and the recessus scalae tympani. But the pars canalicularis, which is fairly completely chondrified at this stage, still displays a blastematous roof for the crus commune and the recessus utriculo-ampullaris posterior. The floor of the lateral recess is also procartilaginous in the 7.2 mm embryo. Although I could not distinguish definite chondrification centres, the condition of the cartilage of the otic capsule at this stage strongly suggests the participation of at least two centres, one of which occurs in the pars canalicularis and the other in the anterior part of the floor of the pars cochlearis. Chondrification spreads rapidly from these centres and continuity is very soon established.

In the 8.4 mm embryo the cartilage of the otic capsule shows the following deficiencies: A procartilaginous posterior portion of the crista falciformis and a procartilaginous posterior portion of the base of the cavum supracochleare. The processus recessus is also still deficient at this stage resulting in the confluence of the jugular foramen and the apertura medialis of the recessus scalae tympani. Actually the parts of the fissura metotica in Suncus are not differentiated till after the 9.5 mm stage when the processus recessus and the postero-medial wall of the recessus scalae tympani acquire cartilaginous continuity with the postero-lateral border of the basal plate. Although still procartilaginous in the 8.4 mm embryo the roof of the crus commune and recessus utriculo-ampullaris posterior are chondrified in the 9.5 mm embryo leaving an extensive endolymphatic foramen. Not till the 15.6 mm stage does a separate foramen for the lower nerve to the saccule become isolated.

The suprafacial commissure is slightly chondrified in the 7.2 mm embryo but the foramen faciale secundarium is not surrounded by cartilage till the 9.5 mm stage.

The parietal plate chondrifies very early and, although arising from a separate centre, it acquires continuity with the otic capsule at a very early stage of

VOL 28 194

its development. In the 6.8 mm embryo the parietal plate already shows a slight degree of chondrification and is in blastematous continuity with the otic capsule. In the 7.2 mm embryo the commissura parieto-capsularis anterior is entirely chondrified. The cartilage of the parietal plate does not join the supra-occipital till the 8.4 mm stage. Similarly the anteriorly directed spur of the parietal plate does not develop until very late, being absent in the 9.5 mm embryo. In the 8.4 mm stage an extremely small splint-like strip of cartilage lies just anterior to the parietal plate. This splint is incorporated in the parietal plate in the 9.5 mm stage without, however, forming any conspicuous anteriorly directed spur.

Both the crista parotica and the opercular process develop in cartilaginous continuity with the pars canalicularis. The crista parotica is the first to develop and is already partly chondrified in the 7.2 mm embryo. From the crista parotica the chondrification spreads into the opercular process with which it is in blastematous continuity. In the 8.4 mm embryo the opercular process is extensively chondrified. I could find no connections during development (either cartilaginous or blastematous) between the opercular process and the slight anterior prolongation of the supraoccipital. On the contrary, it was found that the opercular process develops at an early stage in situ and in continuity with the otic capsule whereas the anterior prolongation of the supraoccipital (see later) develops as an outgrowth from the supraoccipital cartilage itself. From the material at my disposal I could not therefore, confirm DE BEER's theory on the origin and homology of the opercular process, which apart from Suncus, has also been reported to exist in Sorex and Talpa. Probably the opercular process of these forms has a precursor in the limbus precapsularis described by DE BEER and FELL (1936) in a 9.4 mm embryo of Ornithorhynchus.

The anterior spur of the tegmen tympani which projects forwards over the fossa incudis does not chondrify before the 15.6 mm stage.

The caudal tympanic plate was found to be absent in the 9.5 mm stage but a dense membrane is present as its precursor. In the 15.6 mm embryo the caudal tympanic plate was already slightly chondrified and in cartilaginous continuity with the otic capsule but there seems to be no doubt that it chondrifies in continuity with the otic capsule and not from a separate centre.

d. *Post optimal changes in the auditory capsule:* The cartilaginous auditory capsule ossifies to form the periotic bone which is also known as the petrosum or pars petromastoidea. In the juvenile Suncus the periotic bone is still separate and is not fused either with basioccipital, basisphenoid or with the more laterally situated dermal elements. It is, however, in slight bony continuity with the paracondyloid process of the exoccipital just posterior to the jugular foramen.

The anterior end of the supraoccipital is not fused with the otic capsule but is attached by a tough ligament to the prominentia semicircularis superior (anterior). Between the fused ex- and supraoccipital and the periotic is the long vertically placed mastoid foramen.

The bony auditory capsule very closely resembles the cartilaginous one except that shortly after birth the parietal plate is entirely resorbed and therefore has no counterpart in the bony auditory capsule. It is, however, possible that the extreme posterior end of this plate which is fused with the supraoccipital may be retained and ossified in continuity with this bone.

The otic capsule ossifies, as usual, from several centres. ANDRES (1924) reported 10—12 ossification centres in the otic capsule of the pig. These centres can be separated into two main groups. STADTMÜLLER regards the anterior inner centre which forms the pars petrosa of the otic capsule as the probable homologue of the prootic bone of lower Vertabrates, while the posterior outer centre which forms the pars mastoidea of the adult otic capsule represents the probable homologue of the epiotic and opisthotic of lower forms. In Suncus three main ossification centres could be distinguished in the otic capsule. These centres all make their appearance between the 15.6 mm and 18.3 mm stages. In the 18.3 mm embryo the most anterior and ventral centre was found in the anterior end of the cochlear capsule. This part of the otic capsule is only perichondrally ossified at this stage, but the perichondral ossification was found to be more extensive on the inside of the otic capsule, where it chiefly involves the spiral lamina, than on the outside. The second ossification centre in Suncus was found in the antero-dorsal side of the otic capsule medial to the fossa incudis and the sulcus facialis. It affects the entire region round the foramen faciale secundarium including the whole of the secondary suprafacial bridge. Medially the ossification spreads to the posterior part of the floor of the cavum supracochleare including the postero-dorsal end of the primary suprafacial commissure, while posteriorly it extends into the lateral wall of the vestibular portion of the pars cochlearis surrounding the fenestra ovalis on its anterior and dorsal sides.

An extensive postero-ventral ossification centre was found in the extreme posterior end of the cochlear capsule surrounding the cavum perilymphaticum and the recessus scalae tympani. This centre in the 18.3 mm embryo involves the major part of the processus recessus and it completely surrounds both the fenestra rotunda and the apertura medialis of the recessus scalae tympani. Dorsally this ossification spreads into the floor of the posterior end of the pars canalicularis whilst laterally it spreads into the processus tympanicus petrosi caudalis (see later). In the 22 mm embryo the major part of the otic capsule was found to be ossified and the aforementioned centres are all fused with one another and are all inseparably incorporated in the periotic bone. The tegmen tympani was found to ossify in continuity with the rest of the crista

VOL
28
194

parotica as is the case with the tympano-hyale. Usually the tympano-hyale ossifies from an autogenous centre near the otic capsule so that its bony fusion with the crista parotica to form the processus hyoideus (FRANCK) is secondary. PARKER (1885) mentioned that in several Insectivores the proximal part of the tympano-hyale ossifies in continuity with the periotic, similarly FLOWER (1871) mentioned that the same condition may prevail in the sheep.

The opercular process in Suncus has a definite autogenous ossification centre which does not fuse with the rest of the otic capsule until shortly after birth.

The postero-dorsal canalicular part of the otic capsule ossifies fairly late. In the 22 mm embryo a separate ossification centre could be distinguished in the prominentia subarcuata superior externa. This ossification centre later involves the cartilaginous protection for the canalis semicircularis superior (anterior) and fuses with the ossification spreading from the rest of the otic capsule into the prominentia semicircularis posterior. The prominentia utriculo-ampullaris anterior and the prominentia semicircularis are the last portions of the otic capsule to ossify being cartilaginous even for some time after birth. During the later stages of development the large parafloccculus is firmly enclosed in the periotic bone. The part of the periotic bone which encloses the parafloccus shows two foramina in its posterior ventro-lateral aspect, the one lying behind the other. These foramina, however, transmit no bloodvessels or nerves.

The caudal petrosal tympanic plate in Suncus ossifies very early. Even in the 18.3 mm embryo its major part is ossified, not from a separate centre but in continuity with the otic capsule. During the later stages of intra-uterine development and also after birth this bony plate (which may be called the processus petrosi caudalis) grows still larger and forms a small bulla which completely hides the foramen rotundum and the posterior extension of the middle ear. It is not closely related to either the squamosal or the tympanic (ectotympanic) bone, but it extends so far forward as to overlap the posterior end of the fenestra ovalis and practically to touch the posterior end of the processus hyoideus. The antero-dorsal end of the processus tympanicus petrosi caudalis bears a slight notch through which the stapedius muscle leads backwards from its attachment to the stapes. The foramen caroticus posterius lies immediately in front of the antero-ventral aspect of this petrosal plate.

VAN DER KLAAUW (1929), in a paper on the tympanic region of the skull in the Macroscelidae, describes a caudal petrosal plate which participates in the formation of the base of the auditory bulla. He also mentions in this paper that the caudal petrosal plate is formed relatively early in the embryo, being still cartilaginous in the youngest specimen investigated by him. For this reason VAN DER KLAAUW hesitates to call this plate a real processus tympanicus petrosi since VAN KAMPEN (1905, p. 452 and 1904, p. 127) maintained that

the petrosal plate in the Insectivora does not seem to develop in cartilage. I quote from VAN KAMPEN (1904, p. 127): "Eerder sou men m.i. nog de lyst van het petrosum die by vele Insectivores den achterwand der trommelholte vormt, voor een entotympanic kunnen aansien èn om haar ligging t.o. van het petrosum èn om de overeenkomst met sommige Marsupiale. Een kraakbenige aanleg schijnt se niet te bezitten: WIŃCZA (1896) heeft by verschillende Insektivoren (Erinaceus, Ericulus, Centetes) geen kraakbeen in den wand der trommelholte kunnen ontdekken." This is no serious objection since it was demonstrated in Suncus that the cartilaginous caudal petrosal plate is formed fairly late in ontogeny as compared with the rest of the chondrocranium, and furthermore, that soon after its formation it becomes ossified. Never is the cartilaginous petrosal plate as extensive as the osseous plate so that it is quite possible that the brief cartilaginous stage in the development of this plate was not represented in the embryonic stages investigated by VAN KAMPEN and WIŃCZA. It may even be possible that the short preformation in cartilage may be entirely omitted in the ontogenetic development of this structure in some Mammals without, however, affecting its homology. Similar conditions are often found in the alisphenoid and to a certain extent also in the orbitosphenoid.

Both a rostral and a caudal entotympanic are absent in Suncus.

3. The Ala Temporalis (figs. 1 and 2) is a nearly horizontal plate in Suncus. At its optimal stage of chondrification it is joined to the lamina hypophyseos by the processus alaris and to the cochlear capsule by the alicochlear commissure. It is directed antero-laterally and bears two main processus. The antero-lateral process is the larger of the two and is pierced by the foramen ovale which transmits the mandibular nerve. Its antero-lateral edge has a slight dorsal inclination. This process is probably the same as the processus ascendens in other forms although one can hardly speak of a lamina ascendens at this stage in Suncus. The anterior process (FAWCETT) or pterygoid process is directed antero-medially and has a slight ventral inclination. Its medial border is invaded by the postero-lateral edge of the pterygoid bone which, at this stage, still bears a nodule of secondary cartilage at its anterior end.

The ala temporalis forms a considerable part of the floor of the cavum epitericum and, lying over its dorsal surface, is the Casserian ganglion. In Suncus the ala temporalis does not enclose a foramen for the transmission of the maxillary division of the trigeminal nerve.

a. *Early development of the ala temporalis:* As already stated the ala temporalis in Suncus chondrifies from a separate centre although in blastematous continuity with the central stem at an early stage of its development. DE BEER (1929, p. 454) gives a list of Mammals in which the ala temporalis arises separately and he also mentions a few forms (Sorex, Echidna, Talpa

VOL.
28
194

and Ovis) in which it chondrifies in continuity with the processus alaris. The latter condition is regarded as being in all probability a secondary manifestation.

In the 7.2 mm embryo the ala temporalis is entirely blastematous although the posterior portion, and especially the base of the pterygoid process is densely procartilaginous. The latter part of the ala temporalis is the first to chondrify (in the 8.4 mm embryo) and from this centre the chondrification spreads in three directions, viz: antero-medially into the pterygoid process, antero-laterally into the antero-lateral process and postero-medially towards the processus alaris and alicochlear commissure (fig. 11). Cartilaginous connections with the processus alaris and alicochlear commissure, however, are not established until shortly after the 9.5 mm stage. The pterygoid process and the pterygoid cartilage, although in blastematous continuity, are at no stage of their development in cartilaginous continuity as in Sorex.

b. *Post optimal changes in the ala temporalis:* The ala temporalis ossifies to form the greater part of the alisphenoid bone in the adult. Already in the 15.6 mm embryo of Suncus two ossification centres could be distinguished (figs. 1 and 2). The larger ossification centre surrounds the fenestra ovalis while a smaller centre could be distinguished in the anterior tip of the medial pterygoid process. The centres rapidly expand and join one another, leaving the basal portion of the ala temporalis (which is fused with the processus alaris and the alicochlear commissure) un-ossified till in the juvenile animal when the alisphenoid becomes thereby fused with the basisphenoid. The pterygoid process of the ala temporalis is completely ossified and indistinguishably fused with the posterior end of the pterygoid bone in the 18.3 mm embryo. The larger antero-lateral process of the ala temporalis shows a narrow strip of cartilage along its upper edge in the 18.3 mm embryo (fig. 4). This outer part of the alisphenoid which is pierced by the fenestra ovalis (or "canalis ovalis") is thick especially along its upper edge. This edge of the alisphenoid is vertically placed and it is fused with the ventral edge of the pars entoglenoidea squamosi in this region thus participating in the formation of the postero-ventral shelf of the glenoid fossa for the jaw joint. In Marsupials the alisphenoid may also take part in the formation of the glenoid fossa. The vertically placed anterior end of the alisphenoid extends far forward. It is thin, not pneumatic and ventrally it is closely related to the posterior end of the palatine and the orbitosphenoid. The greater part of this anterior end of the alisphenoid grows out like a dermal bone from the rest of the alisphenoid and is therefore not preformed in cartilage. This is not extraordinary in Mammals. CORDS (1915) reports that in Didelphys the alisphenoid ossifies wholly in membrane while in Perameles it is partly preformed in cartilage. DE BEER (1937), discussing the possibility of membrane bones becoming transformed into cartilage bones and vice versa, drew attention to the condition

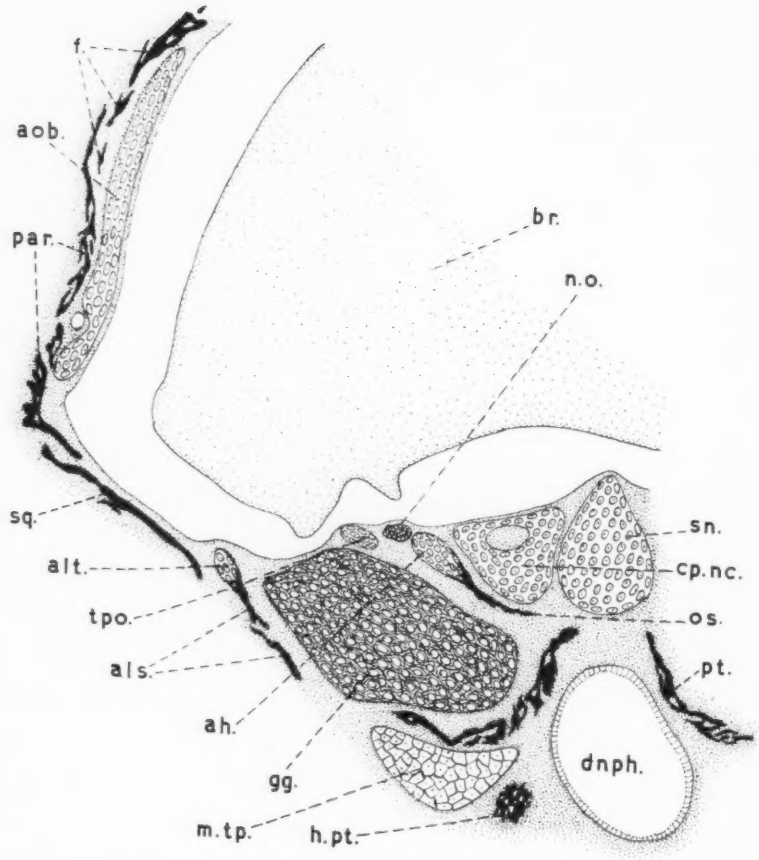

Fig. 7. Transverse section through the orbitosphenoidal region of the skull of an 18.3 mm embryo (× 45).

frequently found in the vertebrae of Teleostei where the basidorsal and basiventral cartilages may fail to chondrify so that the bony vertebra ossifies directly from mesenchyme. This, however, does not affect the homologies of the structures concerned. In the juvenile Suncus the extreme posterior end of the alisphenoid, which is fused with the basisphenoid, contributes to the formation of the dorsomedial wall of the anterior end of the middle ear, although one can hardly speak of a processus tympanicus alisphenoidei at this stage.

4. The ala orbitalis (figs. 1, 2, 8, 9 and 10) forms an important part of the lateral wall of the primordial cranium. It is a large triangular cartilage the base of which is directly dorsally. The anterior basal angle of the ala orbitalis is attached to the frontal prominence of the pars intermedia of the nasal capsule by a fairly broad commissura sphenethmoidalis. The

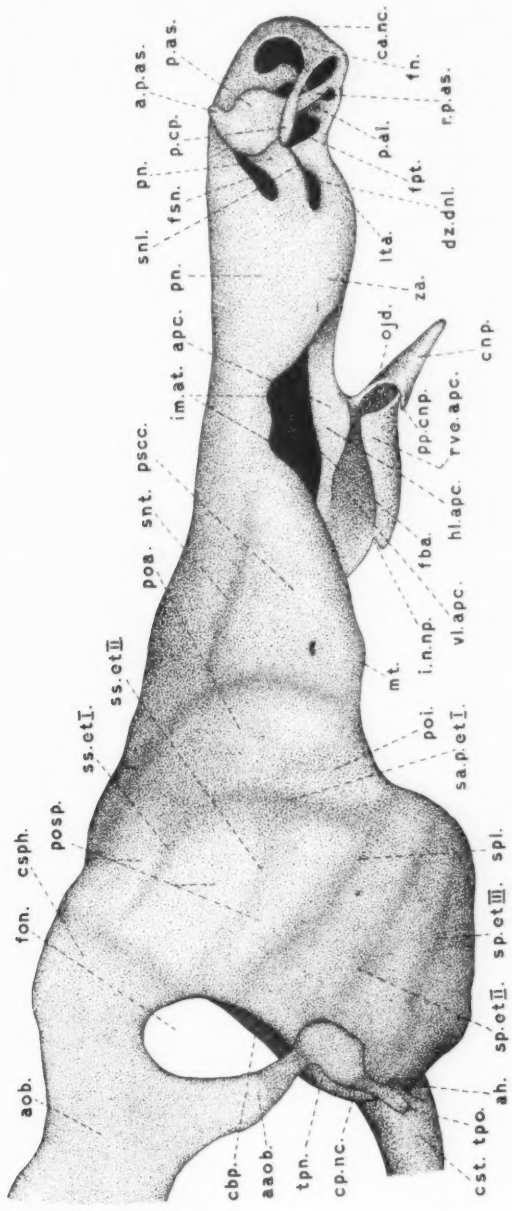

Fig. 8. Lateral view reconstruction of the nasal capsule of an 18.3 mm embryo of *Sancus orangiae* (× 30).

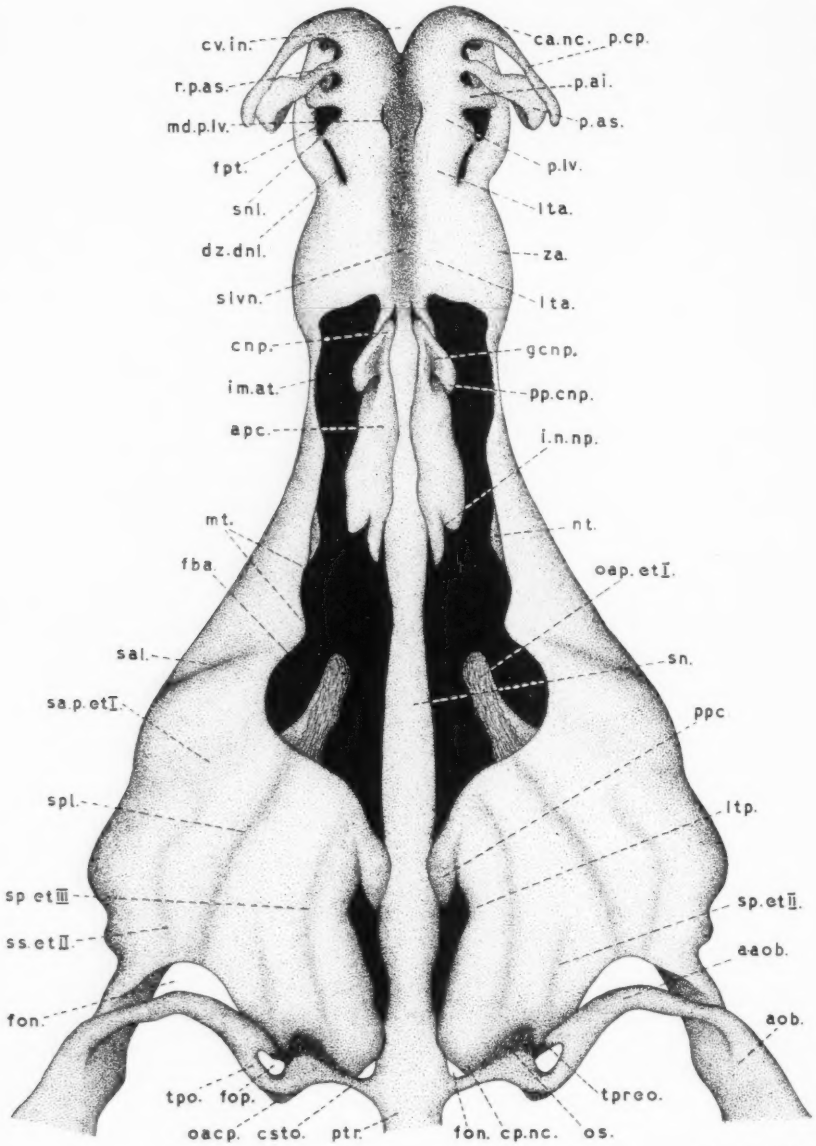

Fig. 9. Ventral view reconstruction of the nasal capsule of an 18.3 mm embryo (× 30).

posterior basal angle of the ala orbitalis which, in Mammals, is usually attached to the parietal plate by the commissura orbitoparietalis, extends backwards for some distance as a stout and broad plate which roofs over the extensive spheno-parietal fontanella antero-dorsally. A considerable space remains between this process and the anteriorly directed spur of the parietal plate. The

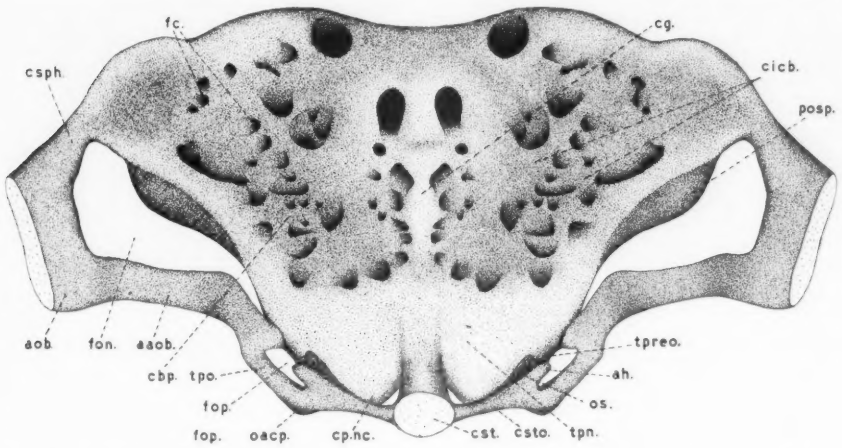

Fig. 10. Posterior view of a wax model reconstruction of the nasal capsule of an 18.3 mm embryo (× 30).

apex of the ala orbitalis has the shape of a slender rod which is directed downwards, forwards and medialwards. It bifurcates into a taenia preoptica (v. taenia antoptica or preoptic root of the ala orbitalis) which leads medialwards anterior to the optic nerve, and a taenia postoptica (v. taenia metoptica or postorbital root of the ala orbitalis) which leads to the trabecular plate behind the optic nerve. In Suncus, however, this bifurcated apical portion of the ala orbitalis is more coronally placed (fig. 10) so that the taenia preoptica lies antero-medial to the optic nerve and rests on the postero-lateral aspect of the cupula posterior of the nasal capsule and the taenia postoptica lies postero-lateral to the optic nerve. The optic foramen in Suncus is displaced laterally and directly ventro-medial to it the pre- and postoptic roots of the ala orbitalis fuse to form a slender rod-shaped attachment to the trabecular plate. The taenia preoptica is extremely delicate and at this stage it is partly ossified. From the anterior edge of the taenia preoptica and the common attachment of the taeniae opticae a short spur, probably corresponding to the ala minima described in Didelphys and Talpa, projects forward and lies against the postero-ventral aspect of the cupula posterior of the nasal capsule (figs. 9 and 10).The floor of the optic foramen is formed by a small spur of cartilage corresponding to the ala hypochiasmata in other forms (fig. 10). This little spur is free laterally but its medial end is fused with the ala orbitalis ventro-medial to the optic foramen. The ala hypochiasmata in Suncus lies on the nasal capsule. It was first described in a Mammal (the rabbit) by VOIT who held it to be homologous with the ala hypochiasmata in Lacerta. It has since been described in several other Mammals (see STADTMÜLLER 1936).

The anterior border of the ala orbitalis is separated from the nasal capsule by the fissura orbito-nasalis (or the ethmoidal fissure) through which the

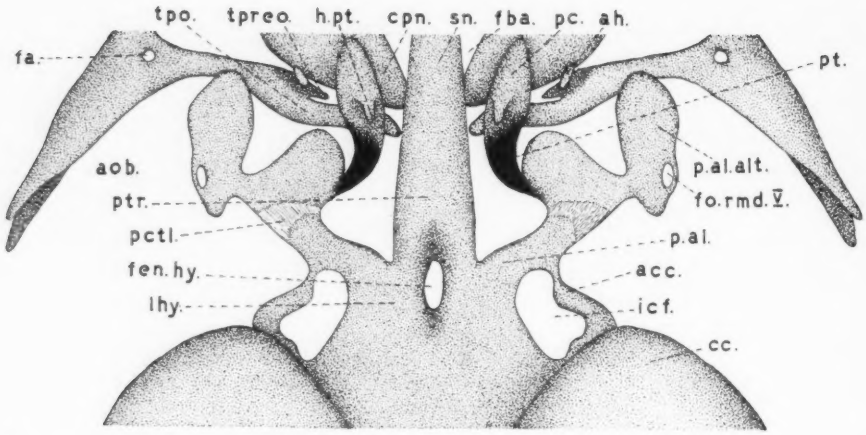

Fig. 11. Ventral view reconstruction of the sphenoidal region of the chondrocranium of a 9.5 mm embryo (× 40).

ramus ophthalmicus profundus of the trigeminal nerve leaves the orbit and enters the supracribrous recess. In Suncus this fissure is divided into a spacious dorso-lateral division and a compressed ventro-medial division (fig. 10) due to the intimate relations of the ala hypochiasmata, preoptic root and common medial stem of the pre- and postoptic roots with the nasal capsule. This undoubtedly resembles the condition in some Mammals (Didelphys and Talpa) where the ventro-medial portion of the orbitonasal fissure becomes isolated as a foramen prechiasmaticum due to the growth of an ala minima from the preoptic root. For the development and relations of the foramen prechiasmaticum in other Mammals, viz. Poikilophoca, Felis, Xerus, Mustela and Primates the reader is referred to STADTMÜLLER (1936).

a. *Early development of the ala orbitalis:* The ala orbitalis in Suncus chondrifies separately as is usual. The first evidence of chondrification is found in the 7.2 mm embryo and in the 8.4 mm stage it is already confluent with the nasal capsule through the commissura sphenethmoidalis. The connection with the central stem, however, is not established until after the 9.5 mm stage. The ala hypochiasmata in Suncus also chondrifies from a separate centre and does not fuse with the ala orbitalis until fairly late (fig. 11).

b. *Post optimal changes in the ala orbitalis:* The greater part of the ala orbitalis ossifies to form the orbitosphenoid in the adult. This ossification takes place in the medial or apical portion of the ala orbitalis. The basal portion and the adjoining commissura sphenethmoidalis are completely resorbed in the juvenile and have no counterpart in the adult orbitosphenoid. Ossification of the orbitosphenoid commences from a centre in the medial part of the slender preoptic root. This ossification centre can be distinguished in the 15.6 mm embryo (figs. 7, 9 and 10). It expands rapidly medialwards into the ala

VOL
28
194

VOL.
28
947

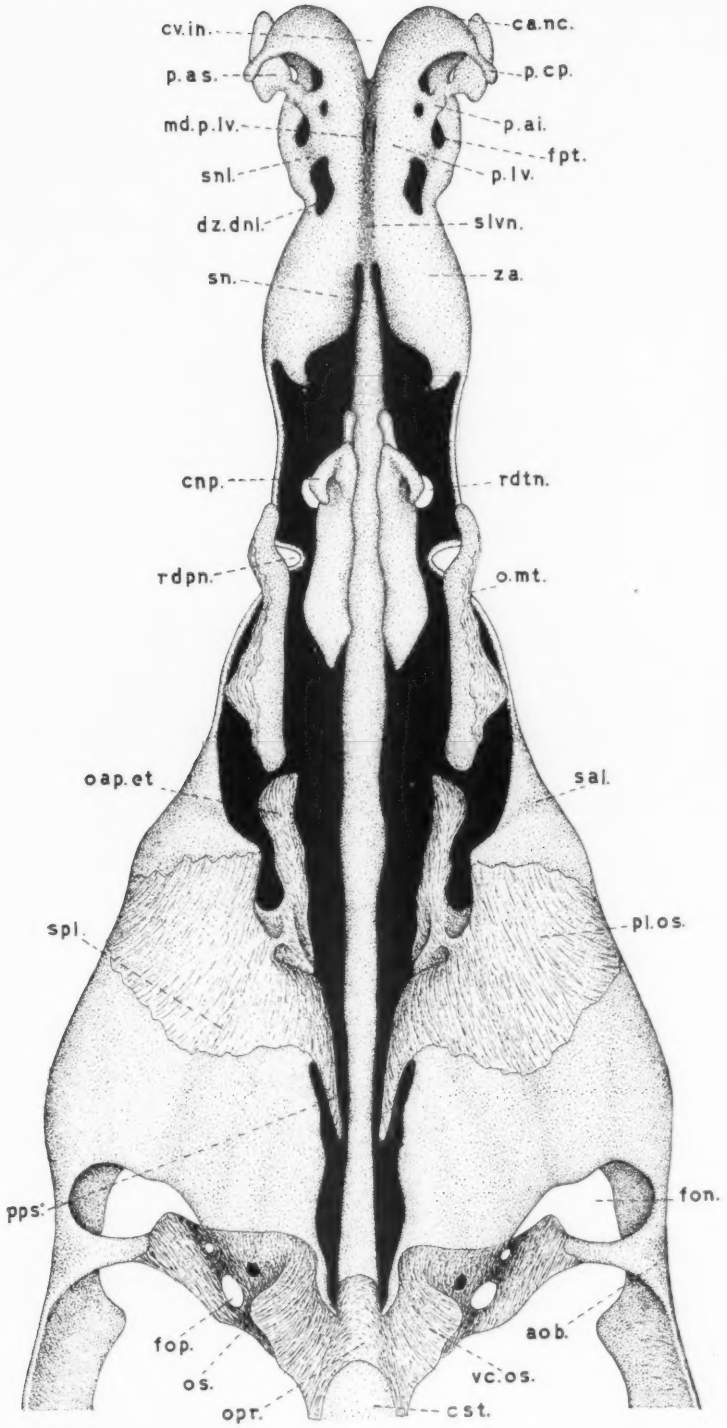

Fig. 12. Ventral view reconstruction of the nasal capsule of a 25.5 mm embryo—indicating the position and extent of ossification centres present at that stage (× 22).

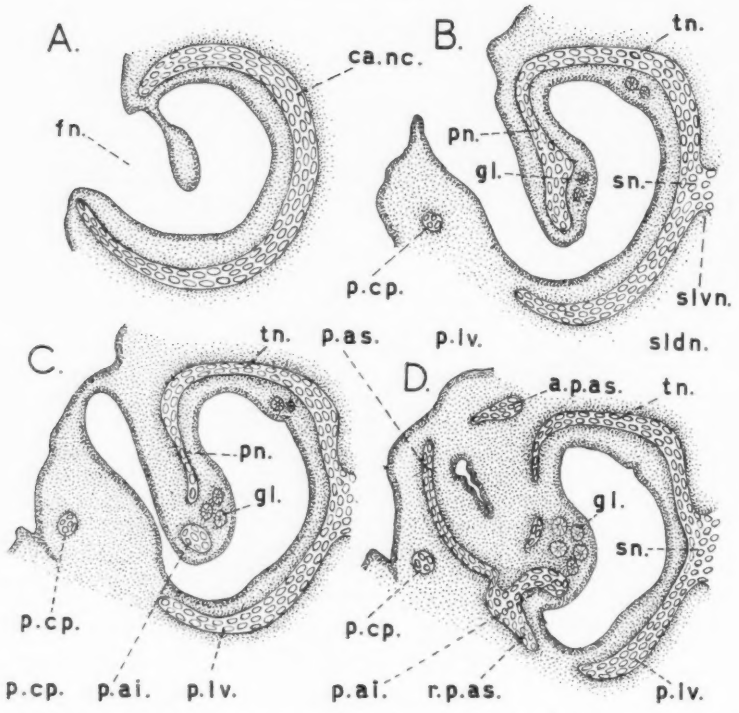

Fig. 13 A—D. Consecutive transverse sections through the tip of the snout of an 18.3 mm embryo (× 65).

hypochiasmata and the common attachment of the optic roots to the central stem. The short anterior clinoid process of the postoptic root seems to ossify from a separate centre which can be clearly recognised in the 18.3 mm embryo (figs. 9 and 10). The greater part of the orbitosphenoid medial to the optic foramen grows outwards from the slender ala orbitalis in dermal bone fashion until it covers the major part of the cupula posterior of the nasal capsule from its lateral, posterior and ventral sides. Due to the absence of a separate presphenoid ossification in Suncus the two orbitosphenoid ossification expand medialwards and become confluent in the midventral line to take the place of the presphenoid. This median fusion of the two orbitosphenoids is first observed in the young Suncus measuring 28.5 mm. Similar conditions have been reported for several other Mammals (see STADTMÜLLER 1936, p. 912 and 913). This condition does not necessarily signify that the presphenoid is totally absent in Suncus. It is possible that the presphenoidal part of the orbitosphenoid represents the true presphenoid, although a separate centre never develops. Ventral to the cupula posterior of the nasal capsule the orbitosphenoid bears a conspicuous crest which is directed downwards and outwards and is closely related to the alisphenoid and the posterior tip of the

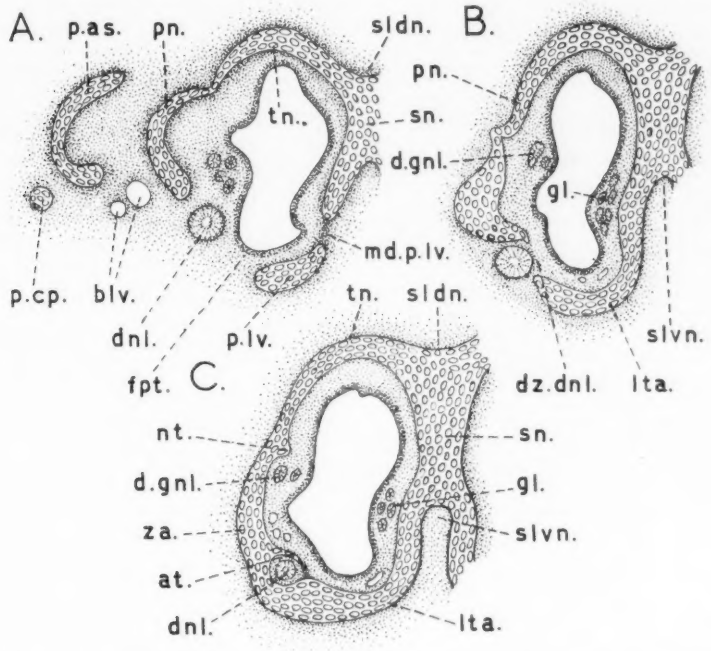

Fig. 14 A—C. Consecutive transverse sections through the nasal capsule near the tip of the snout of an 18.3 mm embryo (× 65).

palatine (fig. 12). The orbitosphenoid forms the entire covering of the cupula posterior of the nasal cavity during later development, since the greater part of the cartilaginous nasal capsule of this region is resorbed and not replaced again by the mesethmoid ossification. In several places the orbitosphenoid becomes indistinguishably fused with the mesethmoid.

In the juvenile Suncus the foramen rotundum was found to be confluent with the large and fissure-like foramen sphenorbitale or foramen lacerum anterius so that this common foramen transmits both the maxillary and ophthalmic branches of the trigeminal nerve together with the oculomotor, trochlear and abducens nerves. Both the alisphenoid and the orbitosphenoid takes part in the formation of this large common foramen.

5. The nasal capsule (figs. 8—10 and 13—22). In the 18.3 mm embryo its length is at least half the total length of the primordial cranium. In the midline the nasal capsule is connected to the chondrocranium through the nasal septum which represents the intranasal portion of the pars trabecularis. Dorso-laterally it is connected to the ala orbitalis by means of the sphenethmoidal commissure. Viewed from the dorsal side the posterior part of the nasal capsule, lodging the turbinals, is much widened thus giving the nasal capsule the characteristic pear-shape of Mammals. The backward extension

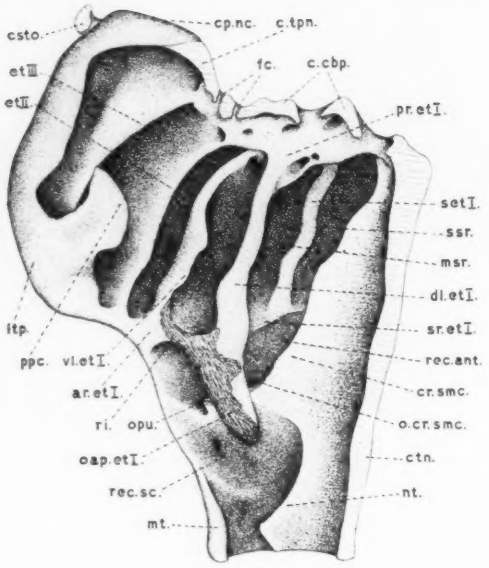

Fig. 15. Medial view of a wax model reconstruction of the pars olfactoria of the nasal capsule of an 18.3 mm embryo (× 30).

of the nasal sac results in the establishment of relations between the posterior division of the nasal capsule and the apex of the ala orbitalis thereby leading to synchondrotic fusion or merely to apposition of the parts concerned.

Only an exceptionally small portion of the roof of the nasal capsule is subcerebral, the precerebral portion being long and slender. This is a primitive feature in Suncus since the precerebral position of the cribriform plate of the nasal capsule is the condition found in non-mammalia.

External aspect of the nasal capsule: The nasal capsule, excluding the septum, can be divided both externally and internally into three parts viz: pars posterior, pars intermedia and pars anterior. The boundaries will presently be described. This division is made partly for convenience but there is also some ontogenetic justification for its introduction into descriptive morphology (STADTMÜLLER 1936, p. 860).

The tectum nasi. Since the subcerebral portion of the nasal capsule is very short its posterior part is steeply inclined ventrally (fig. 8). This inclined portion, which is situated in front of rather than under the brain, has the form of a wide triangle whose apex is directed postero-ventrally while the base forms the anterior border between the pars intermedia and the pars anterior (fig. 10). The true tectum of the pars posterior and pars intermedia, therefore, is formed entirely by the two laminae cribrosae. It faces backwards rather than upwards. It is well fenestrated and these foraminae cribrosae, transmitting the fila olfactoria, are all directed downwards and forwards. The postero-dorsal edge of the septum nasi separates the two cribriform plates and forms a low and rather inconspicuous crista galli (fig. 10). The crista intercribrosa (corresponding to the attachment of the posterior root of the first primary ethmoturbinal which divides the cribriform plate into an antero-lateral and a postero-median portion) can hardly be called a "crest" in Suncus as it does not project sufficiently above the plane of the cribriform plate to form even the slightest ridge externally. The tectum nasi posterius covers only the caudal portion of

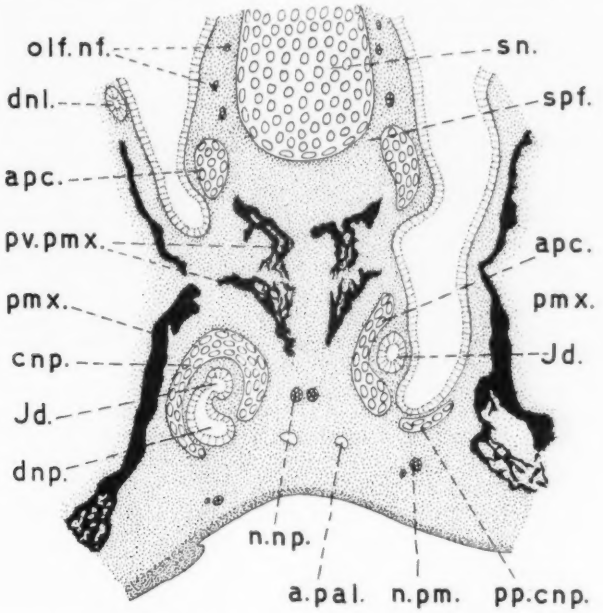

Fig. 16. Transverse section through the region of the nasopalatine cartilages of an 18.3 mm embryo (× 90).

the pars posterior of the nasal capsule. It is more horizontally placed than the bulk of the cribriform plate and makes a blunt angle with this plate over the mid-dorsal aspect of the pars posterior. Medially the tectum posterius is fused with the septum nasi.

The two cribro-ethmoidal foramina are situated immediately lateral to the crista galli near the extreme anterior border of the subcerebral part of the tectum nasi.

The pars anterior of the tectum nasi slopes gently downwards and forwards (fig. 8). Medially it is fused with the nasal septum and laterally it is completely fused with the upper edge of the paries nasi. The foramen epiphaniale is absent as in Elephantulus (DU TOIT 1942) , Sorex (DE BEER 1929) and Erinaceus (FAWCETT 1918 a). The upper edge of the nasal septum in the pars anterior forms the base of the sulcus dorsalis nasi. This sulcus, though shallow over the posterior division of the pars anterior, gradually deepens anteriorly where it eventually leads into the cavum internasale between the cupulae anteriores.

The paries nasi is complete except for the anterior division of the pars anterior which is deficient in several places.

The three regions of the paries nasi can be clearly distinguished.

The pars posterior, the smallest of the three divisions, is separated from the pars intermedia by the postero-lateral sulcus which runs forwards and down-

wards to the lower border of the paries nasi (fig. 8). This sulcus corresponds to the internal attachment of the middle and anterior roots of the first primary ethmoturbinal. The pars posterior projects down below the level of the nasal septum and its lower edge is continued into the lamina transversalis posterior. Posteriorly the paries nasi curves medialwards to form the cupula posterior and postero-dorsally it becomes indistinguishably fused with the lateral edge of the lamina cribrosa.

The pars intermedia projects far laterally. It is bounded anteriorly by the antero-lateral sulcus which corresponds to the internal attachment of the crista semicircularis. On its outer surface the pars intermedia shows several prominences separated from one another by faint sulci corresponding to the attachment of the turbinal cartilages on its inner surface (fig. 8). The prominences themselves correspond to the internal recesses to be described later. The large prominentia superior (or prom. frontalis, FAWCETT) gives rise to the commissura sphenethmoidalis postero-dorsally. This prominence is faintly subdivided into three minor prominences by two inconspicuous sulci which indicate the attachment of the first and second secondary ethmoturbinals. Anteriorly the prominentia superior is separated from the common prominentia inferior (prom. maxillaris, FAWCETT) and prominentia anterior by a deep vertically placed sulcus which indicates the attachment of the anterior root of the first primary ethmoturbinal. The greater dorsal division of this common prominence corresponds to the anterior recess; its smaller and ill-defined lower portion corresponds to the poorly developed recessus inferior (rec. maxillaris) (fig. 8).

The pars anterior of the nasal capsule is of considerable length but only of moderate height. Dorsally it gradually merges into the tectum nasi anterius and posteriorly the antero-lateral sulcus separates it from the prominentia inferior of the pars intermedia. The posterior third of the inferior border is thickened to form the maxillo turbinal; ventrally, however, this turbinal bears no lamina infra-conchalis as in Lepus (VOIT) and Microtus (FAWCETT) (figs. 8, 9 and 15). The nasolacrimal duct runs over the lateral surface of the prominentia supraconchalis in this region but it is not lodged in a sulcus nasolacrimalis. The attachment of the nasoturbinal produces a slight sulcus on the postero- dorsal aspect of the posterior division of the pars anterior. This sulcus indicates the dorsal limit of the prominentia supraconchalis (fig. 8). At about the middle of the pars anterior the lower border of the paries nasi is incomplete. A wide basal fenestra in this region results. The lower margin of the paries nasi in the anterior division of the pars anterior is continued into the lamina transversalis anterior. The latter structure is joined to the septum medially thus forming a complete zona annularis. The nasolacrimal duct in Suncus does not run forward in a sulcus over the ventro-lateral aspect of the zona annularis but it enters the nasal cavity behind the zona annularis and runs along the inside of the latter structure for some distance

VOL
28
194

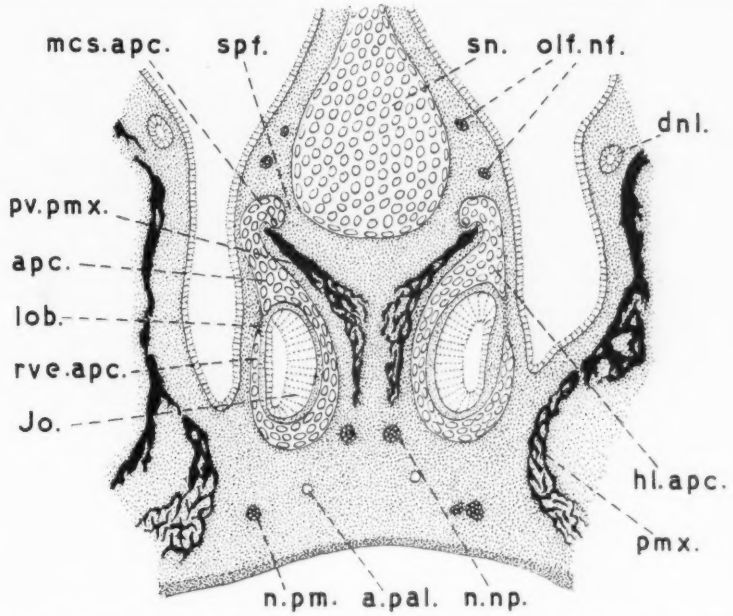

Fig. 17. Transverse section through the region of the "outer bar" of the anterior paraseptal cartilages of an 18.3 mm embryo (× 90).

after which it emerges through an elongated foramen which demarcates the anterior part of the lamina transversalis anterior from the paries nasi. Anterior to this foramen the nasolacrimal duct again enters the nasal cavity through the wide foramen pretransversale (incisura pretransversalis anterior, FAWCETT 1917) (figs. 8 and 14).

The foramen pretransversale is separated from the fenestra naria by a slender bar of cartilage which extends from the processus lateralis ventralis to the antero-ventral corner of the paries nasi. DE BEER (1929) describes a similar cartilaginous bar in Sorex and, judging from its position, it probably represents the processus alaris inferior (STURM 1937).

Terry regards the foramen pretransversale as actually part of the fenestra naria. He calls it the pars lacrimalia to distinguish it from the main anterior portion, the pars atrialis.

Dorsal to the foramen pretransversale there is an elongated fenestra in the paries nasi (fig. 8). This fenestra is covered by dense connective tissue and it has been described in other Mammals under different names viz: fenestra superior nasi (VOIT 1909, DE BEER and WOODGER 1930, DU TOIT 1942), foramen dorsale (FAWCETT 1917, 1918 a and 1918 b) and fenestra lateralis (STURM 1937). Anterior to this fenestra the tectum and paries nasi slope down steeply into the cupula anterior nasi. From the ventro-lateral border of the cupula anterior a long and slender cartilaginous bar projects backwards,

upwards and laterally (figs. 8, 9 and 13). The attachment of this process is identical with that of the processus cupularis or processus alaris medius described by FAWCETT for Erinaceus so that these structures in Suncus and Erinaceus are probably homologous. FAWCETT gives pictures of a processus cupularis anterior in Microtus. It apparently does not correspond with the processus cupularis of Erinaceus and Suncus.

To the posterior tip of the processus cupularis in Suncus a strong tendon is attached which runs along the lateral aspect of the nose. Apart from this tendon, whose muscle pulls the snout laterally, there are two other sets of muscle tendons for the upward and downward movement of the snout. The former is more powerfully developed. The tendons on either side run forward over the dorsal surface of the nasal capsule. Opposite the incisura maxillo-atrioturbinalis they join to form an extensive fascial sheet which roofs the shallow sulcus dorsalis nasi and the tectum nasi. This sheet becomes more compact anteriorly until over the extreme anterior end of the pars anterior it is shaped as a cylindrical tendon lodged at the base of the sulcus dorsalis nasi. It is inserted into the base of this sulcus where it curves downwards between the cupulae anteriores. The two tendons for the downward movement of the snout are also well developed. They run on either side of the nose along its ventro-lateral aspect and converge anteriorly. Opposite the foramen pretransversale each tendon gives off a short dorsal branch which is inserted into the ventro-medial wall of the processus lateralis ventralis. Anterior to this insertion the main portions of the tendons join to form a single tendon in the mid-ventral line. The anterior end of this common tendon turns upwards through the cavum internasale between the two cupulae anteriores and is inserted into the connective tissue over the anterior end of the sulcus dorsalis nasi. The muscles which act through the three sets of tendons described render the tip of the snout extremely mobile. The cupulae anteriores are bound together by two short but strong transverse ligaments which prevent them from being pulled apart by the two laterally acting tendons. These two ligaments are attached to the dorso-medial and ventro-medial aspects of the cupulae anteriores respectively. Besides keeping the two cupulae anteriores together these ligaments also act as a pulley for the ventral tendon which runs over their anterior surfaces in an upward and backward direction.

A further pair of muscle tendons moves the superior alar cartilages. Each one of these is inserted into the postero-dorsal edge of the corresponding superior alar cartilage. From the muscle belly the tendon runs forward over the postero-lateral aspect of the nose.

Considerable confusion existed in the past about the relations of the alar cartilages. HANS STURM (1937) gives a good account of these difficulties and endeavours to establish a satisfactory system of nomenclature. Concerning the alleged function of these cartilages he concluded. "In die Ausbildung der Pro-

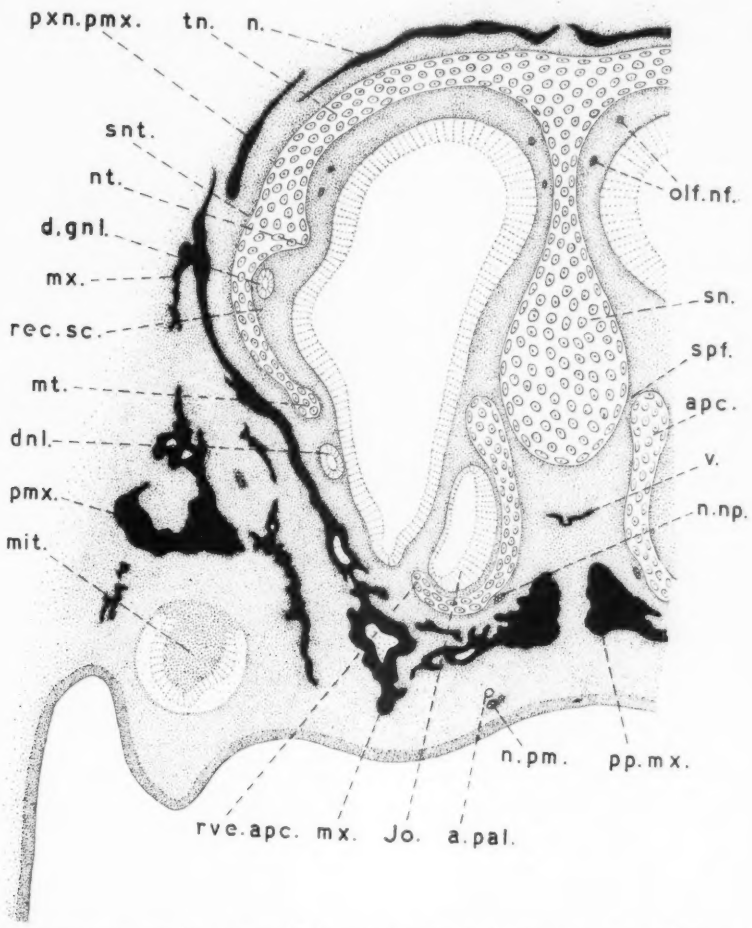

Fig. 18. Transverse section through the nasal capsule of an 18.3 mm embryo—at the level of the posterior ends of the anterior paraseptal cartilages (× 75).

cessus alares superior und inferior können wir das Bestreben sehen den hintersten Absnitt der Fenestra naria, in den der Ductus Nasolacrimalis einmündet, nach vorn zu abzuschliessen" (p. 200).

The processus alaris superior in Suncus is well developed. It lies lateral to the plane of the paries nasi and medial to the processus cupularis. It is directed upwards and backwards. The relations of the processus alaris superior are complicated. Ventrally it arises from a slender root on the antero-lateral corner of the processus lateralis ventralis (figs. 8 and 9). In its postero-dorsal course the root of the processus alaris superior crosses the aforementioned processus alaris inferior with which it is in slight cartilaginous continuity (fig. 13 D). Enclosed between the roots of the processus alares superior and in-

ferior is a small fenestra which does not transmit any bloodvessel or nerve. Near its centre the processus alaris superior is in slight cartilaginous continuity with the paries nasi antero-ventral to the fenestra superior nasi.

A ventral attachment of the processus alaris superior to the processus lateralis ventralis is exceptional but it has been recorded in Sorex by DE BEER and in a young pig embryo by STURM. It may also be present in Microtus but FAWCETT'S description is not clear on this point. In Suncus, therefore, the fenestra naria is bounded anteriorly by the cupula anterior, ventrally by the processus lateralis ventralis, laterally by the processus cupularis and postero-laterally by the root of the processus alaris superior and the processus alaris inferior.

The floor (solum nasi) of the nasal capsule is rather incomplete. The lamina transversalis posterior forms the floor of the pars posterior of the nasal capsule. Posteriorly it is confluent with the floor of the cupula posterior but as a result of the pronounced ventral projection of the pars posterior the lamina transversalis posterior is not horizontally situated. Its medial edge is curved upwards and medialwards (fig. 15) but does not reach the ventro-lateral border of the septum, remaining separated from the latter by an appreciable gap (fig. 9). Fused with the antero-medial aspect of the lamina transversalis posterior is the posterior paraseptal cartilage which therefore, also contributes to the formation of the floor of the pars posterior. The posterior paraseptal cartilage is separated from the nasal septum by a very narrow septo-paraseptal fissure. This cartilage has no anteriorly directed spur but it bears a conspicuous posteriorly directed spur which remains free and is not fused with the lamina transversalis posterior as in Sorex (figs. 9 and 15). In Elephantulus a similar posterior spur was described by DU TOIT who regarded it as part of the lamina transversalis posterior and not as part of the posterior paraseptal cartilage. The middle portion of the nasal capsule has practically no floor thus resulting in an extensive fenestra basalis. The antero-medial portion of the large basal fenestra is partly floored by the anterior paraseptal cartilages which will be discussed in detail later.

Anterior to the basal fenestra the solum nasi is formed by the lamina transversalis anterior. Medially the latter lamina is fused to the ventro-lateral edge of the septum nasi, while laterally it is confluent with the ventral border of the paries nasi. In this way a complete zona annularis is formed (fig. 9). Because of the fact that the lamina transversalis anterior lies at a lower level than the ventral border of the nasal septum a conspicuous sulcus ventralis nasi results. Anteriorly the lamina transversalis anterior is continued into the processus lateralis ventralis (SPURGAT) which again passes over insensibly into the cupula anterior of the nasal capsule (fig. 9). STURM (1937) gives a short historical review of the processus lateralis ventralis and also supplies a list (p. 217) of synonyms used for this structure by certain other authors. The

VOL.
28
194

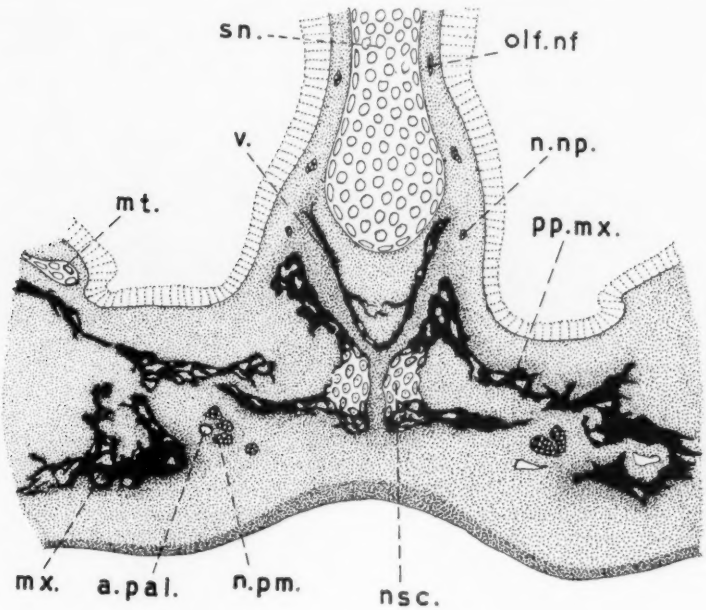

Fig. 19. Transverse section of the hard palate of an 18.3 mm embryo—passing through the maxillary palatine processes (× 90).

recurved lateral edge of the processus lateralis ventralis in Suncus is in cartilaginous continuity with the processus alares superior and inferior. The ascending medial portion of the processus lateralis ventralis which is fused with the nasal septum displays an elongated deficiency which faces the sulcus ventralis nasi.

Posterior to the zona annularis, neither a processus transversalis nor processus maxillaris are present. The vertical or ascending medial border of the lamina transversalis anterior, however, was found to be directly continuous with the anterior paraseptal cartilage.

The anterior paraseptal cartilage (figs. 8, 9 and 16—18) in Suncus is of the more specialised Eutherian type described by BROOM (1915 a and b) and which, inter alia, is also characteristic of the typical Insectivores, i.e. the Lipotyphla. The anterior paraseptal, like the posterior paraseptal cartilage, is separated from the septum nasi by a narrow septo-paraseptal fissure. Posteriorly it ends freely in the basal fenestra so that the two paraseptal cartilages are not directly connected. This seems to be the common secondary condition in Mammals, since a cartilago paraseptalis communis (ZUCKERKANDL) is only found in the following Mammals: Halmaturus (SEYDEL 1896), Lepus (VOIT 1909), Trichosurus (BROOM 1909), Felis (ZUCKERKANDL 1909 and TERRY 1917), Dasyurus (FAWCETT 1917), Microtus (FAWCETT 1917), Xerus (FAW-

CETT 1923), Manatus (MATTHES 1912) and Mycetes (communicated to Prof. STADTMÜLLER 1936, by Prof. FAWCETT).

The anterior part of the cartilago paraseptalis anterior which arises from the vertical medial border of the lamina transversalis anterior has the shape of a slender rod slightly compressed laterally. STURM (1937) regards this slender anterior attachment of the paraseptal cartilage as a strong indication of its separate origin.

The medial portion of the anterior paraseptal cartilage is more complicated. To its antero-ventral edge the cartilago ductus nasopalatini is attached (fig. 8). Dorsally it is slightly roofed by the posterior attachment of the anterior bar which does not end abruptly on the middle portion of the anterior paraseptal cartilage but is continued for some distance backwards lateral to the plane of the vertical lamella. This forms a roof for Jacobson's organ fig. 8). This roof probably corresponds to the horizontal lamina described by STURM who regards it as homologous with the "outer bar" (BROOM). Actually this "horizontal lamina" does not reach the recurved ventral edge of the vertical lamella in Suncus, so that a true "outer bar" as described for other Mammals, where it encircles the origin of Jacobson's duct, does not exist in the 18.3 mm embryo of Suncus. However, the anetrior tip of the recurved ventral edge of the vertical lamella is attached to the "horizontal lamella" by a dense strip of connective tissue which represents the rudiment of the "outer bar" (see later).

The posterior part of the anterior paraseptal cartilage is typically trough-shaped with the ventral border recurved considerably to form a ventro-lateral protection for Jacobson's organ (fig. 8). This region, however, may be completely cylindrical in other Mammals, or it may be entirely flat (see STADTMÜLLER 1936, p. 902). The postero-ventral border of the anterior paraseptal cartilage displays an incisura which transmits the nervus nasopalatinus or Scarpa's nerve (figs. 8 and 9). This nerve is continued forwards in a shallow sulcus along the ventro-medial border of the vertical lamella of the anterior paraseptal cartilage (fig. 18). It passes through the foramen incisivum with the nasopalatine canal and the duct of Jacobson's organ and supplies the anterior portion of the palate. Just before the nasopalatine nerve passes through the incisura in the postero-ventral aspect of the anterior paraseptal cartilage it gives off a delicate branch to the organ of Jacobson itself.

DU TOIT (1942) reported a similar groove which contains a nerve in the vertical lamella of the anterior paraseptal cartilage in Crocidura and although she did not mention it, a similar groove is present in Elephantulus though less conspicuous. The organ of Jacobson in Suncus does not extend back beyond the incisura for Scarpa's nerve.

Cartilago ductus nasopalatini (figs. 8 and 16). Of this structure, STURM (1937, p. 219) gives a good synoptic description. He writes: "Wir verstehen

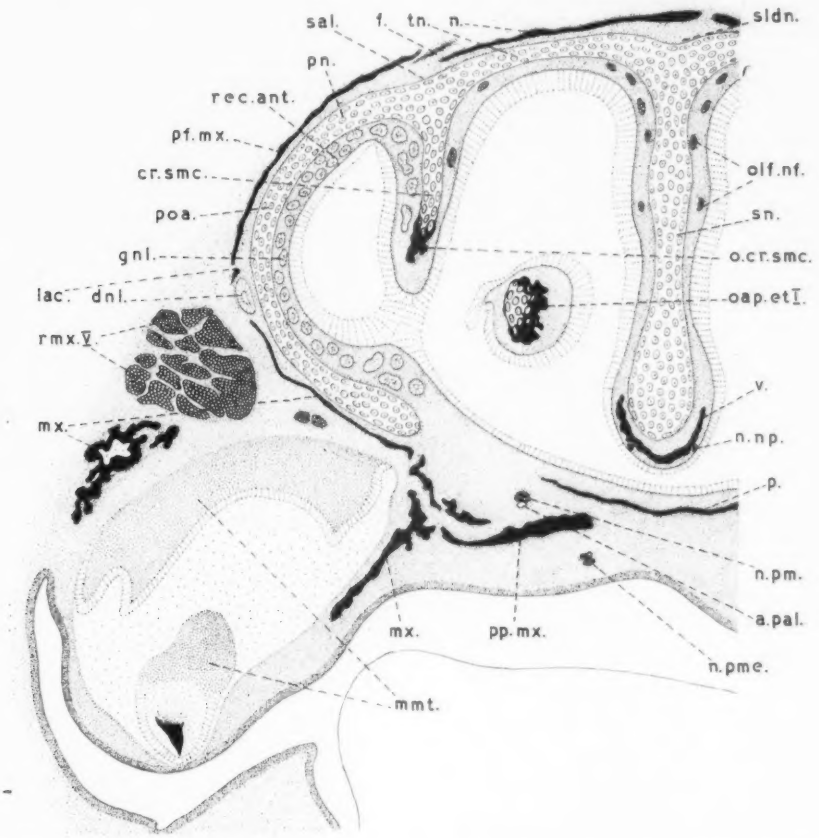

Fig. 20. Transverse section through the nasal capsule of an 18.3 mm embryo—passing through the anterior extremity of the first primary ethmoturbinal (× 50).

hierunter (cartilago ductus nasopalatini) eine Knorpel der den Nasengaumengang von vorn oben und von den Seiten umfassen (sickle-shaped). Er geht in den meisten Fällen nach hinten in den Paraseptalknorpel über seltner ist seine Anheftung an der Vorderkante oder an der Ventralfläche der lamina transversalis. Der knorpel kann isoliert sein." In Suncus this cartilage is well developed and its postero-medial wall is closely fused with the antero-ventral aspect of the anterior paraseptal cartilage. It is directed anteroventrally and has the shape of an inverted tapering trough which surrounds the ductus nasopalatinus dorsally and laterally. The posterior extremity of the ventro-lateral wall of the cartilago ductus nasopalatini projects backwards as a short spur of cartilage which is closely applied to the anterior ventro-lateral aspect of the anterior paraseptal cartilage (figs. 8 and 16). Probably this little car-

tilaginous spur represents a rudiment of the cartilago palatini which is fused with the cartilago ductus nasopalatini as is frequently the case.

Medial aspect of the paries nasi: Medially the paries nasi, especially in the pars posterior and pars intermedia, is characterized by the outgrowth of the turbinal cartilages (fig. 15). These cartilages subdivide the cavum nasi into a series of recesses and are situated approximately at right angles to the plane of the lamina cribrosa. In most Mammals where the lamina cribrosa is chiefly subcerebral and not steeply inclined backwards the turbinals are nearly vertically placed and the recesses between them have a great dorso-ventral depth. In Suncus, however, where the cribriform plates are almost vertical the turbinal cartilages are nearly horizontal, being only very slightly inclined forwards and downwards (fig. 15). Similarly the longitudinal axes of the enclosed recesses run in the same direction as the longitudinal axis of the nasal capsule.

The turbinal cartilages are of two types:

a. Primary ethmoturbinals, also known as major ethmoturbinals or endoturbinals.

b. Secondary ethmoturbinals, also known as minor ethmoturbinals or ectoturbinals.

The pars posterior is separated on its medial side from the pars intermedia by the attachment of the first primary ethmoturbinal. This ethmoturbinal is by far the largest of the three primary ethmoturbinals which are all contained within the pars posterior.

The first primary ethmoturbinal springs from the paries nasi and lamina cribrosa by four roots. The posterior root springs from the lamina cribrosa forming the faint crista intercribrosa at its origin (figs. 10 and 15). The middle and anterior roots are directly continuous. They lie almost in a straight line, their attachments to the paries nasi resulting in the formation of the sulcus posterolateralis externally. The fourth or superior root is vertically placed. It passes upwards from the junctional point of the medial and anterior roots and forms the posterior delimination for the recessus inferior et anterior (fig. 15). The first primary ethmoturbinal is typically bilaminate. Beyond the attachments of its roots the larger upper lamella of the first primary ethmoturbinal projects forwards as a prominent spur. Viewed from the medial side it hides a considerable part of the recessus inferior and anterior from view as well as part of the recessus supraconchalis (fig. 15). The smaller ventral lamella of the first primary ethmoturbinal is concave above. Enclosed between the two lamellae of this ethmoturbinal is a fairly extensive recess which leads upwards and backwards to a set of small olfactory foramina in the cribriform plate.

The secondary primary ethmoturbinal runs parallel to the first. It is much smaller, unilamellar and concave above. Posteriorly it is attached to the lamina cribrosa, laterally to the paries nasi and anteriorly to the recurved anterior border of the pars posterior (fig. 15). Enclosed between the first and second

VOL
28
194

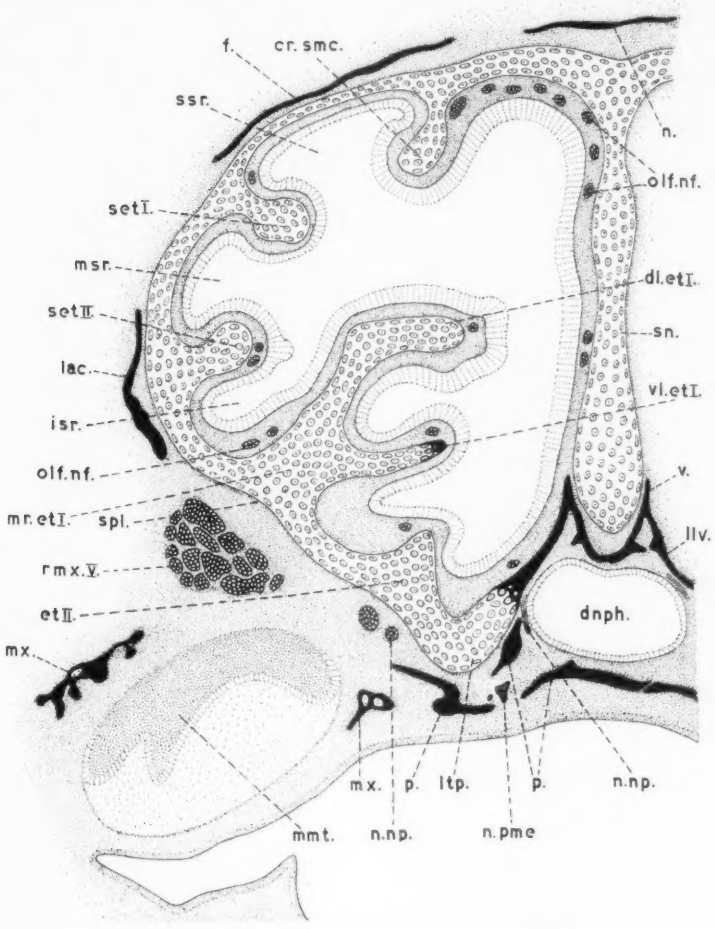

Fig. 21. Transverse section through the nasal capsule of an 18.3 mm embryo—at the level of the lamina transversalis posterior (× 50).

primary ethmoturbinals is a deep recess which, at its base, is subdivided into two secondary recesses by the development of the third secondary ethmoturbinal. This ethmoturbinal is only very small in the 18.3 mm of Suncus (fig. 22).

The third primary ethmoturbinal is of a simple composition and is the smallest of the three. It runs more or less parallel to the second primary ethmoturbinal, is markedly concave antero-dorsally and springs from the posterior ventro-medial aspect of the paries nasi. Anteriorly it does not reach the recurved anterior border of the pars posterior. A deep recess is enclosed between the third and second primary ethmoturbinals which, however, does not lodge any secondary ethmoturbinals at its base. The recessus cupularis lies postero-ventral to the third primary ethmoturbinal and it communicates with

the cavum cranii by two fenestrae olfactoriae. Dorsally the cupular recess is bound by the tectum posterius, posteriorly the cupula posterior of the nasal capsule separates it from the cavum cranii and ventrally this recess is bound by the cupular floor and the lamina transversalis posterior.

The pars intermedia is separated from the pars anterior by the crista semicircularis the attachment of which corresponds externally to the sulcus antero-lateralis. This crista runs obliquely forwards and downwards. Its anterior end bends sharply downwards in front of the recessus anterior and is slightly recurved backwards. The free edge of the crista semicircularis which projects downwards ends abruptly antero-ventrally in a short postero-ventrally directed uncinatus (fig. 15). The base of the crista semicircularis is continued downwards to the free edge of the paries nasi as a faint ridge across the floor of the recessus glandularis. Viewed from the medial side the pars intermedia is largely hidden from view by the free postero-ventral border of the crista semicircularis and the extensive upper lamella of the first primary ethmoturbinal.

The bulk of the pars intermedia is divided into an anterior and posterior division by the vertically placed superior root of the first primary ethmoturbinal. The posterior division of the pars intermedia forms the very deep and far laterally projecting recessus superior (rec. frontalis). Externally it forms the conspicuous prominentia superior (prom. frontalis). Ventrally the floor of this recess is formed by the middle root of the first primary ethmoturbinal. Attached to the base of the recessus superior are the well developed first and second ethmoturbinals (figs. 15, 21 and 22). The free edges of these ethmoturbinals are slightly thickened and they both extend from the cribriform plate behind to the vertical superior root of the first primary ethmoturbinal in front. These two secondary ethmoturbinals subdivide the recessus superior into three secondary recesses viz: superior, middle and inferior. The superior secondary recess is the widest of the three. It faces downwards and is not very deep (figs. 21 and 22). It is enclosed between the crista semicircularis antero-dorsally and the first secondary ethmoturbinal postero-ventrally. Anteriorly this recess communicates with the recessus anterior over the low upper edge of the superior root of the first primary ethmoturbinal (fig. 15). For this reason DU TOIT (1942) probably mistook it for part of the recessus anterior in Elephantulus. The middle secondary recess (anterior secondary recess—DU TOIT) lies between the first and second secondary ethmoturbinals and it is fairly deep. From the prominences caused externally by the superior and middle secondary recesses the commissura sphenethmoidalis arises. The inferior secondary recess lies below the second secondary ethmoturbinal and dorsal to the middle root of the first primary ethmoturbinal. This recess, like the former, is of considerable depth and is entirely hidden from view medially by the upper lamella of the first primary ethmoturbinal.

VOL
28
194

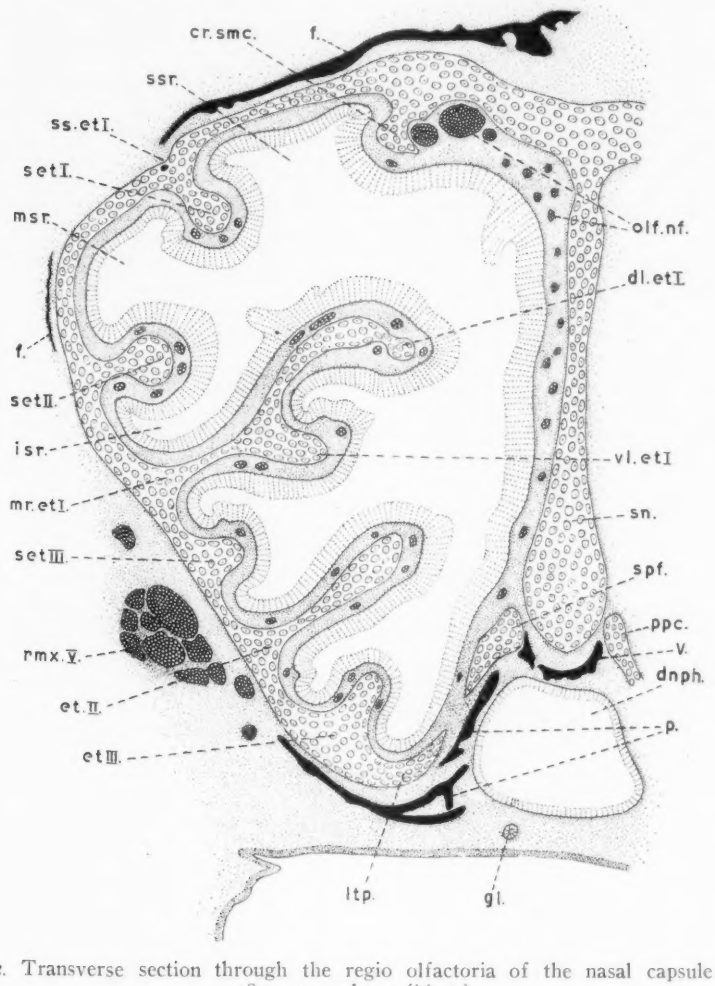

Fig. 22. Transverse section through the regio olfactoria of the nasal capsule of an 18.3 mm embryo (× 50).

The anterior division of the pars intermedia, enclosed between the crista semicircularis anteriorly and the superior and anterior roots of the first primary ethmoturbinal posteriorly, consists of the recessus anterior, recessus inferior (rec. maxillaris) and part of the recessus glandularis. The first of these recesses is vertically placed and it lies under cover of the crista semicircularis (fig. 15). Ventrally it merges into the recessus inferior. The latter recess is rather poorly developed in Suncus. Posteriorly it ends blindly, being bordered by the anterior and superior roots and the upper lamella of the first primary ethmoturbinal (fig. 15). Anteriorly the recessus inferior communicates with the recessus anterior and the recessus glandularis. The latter is rather ill-

defined. FAWCETT (1917, p. 344) said: "It (the recessus glandularis) is not very distinct and it is only definable by modelling in situ the lobules of the said gland (glandula nasalis lateralis)." In Suncus, however, the glandula nasalis lateralis is extensive. It is incompletely divided into two main portions. The greater anterior portion is situated in front of the crista semicircularis and occupies practically the whole of the recessus supraconchalis above the maxilloturbinal. The posterior division of the glandula nasalis lateralis occupies the junctional region between the recessus inferior and the recessus superior. From this point it extends backwards and lines the entire recessus inferior. It also projects forwards and upwards under the most forwardly projecting part of the crista semicircularis, thus filling a great part of the recessus anterior (fig. 20). The posterior division of the glandula nasalis lateral is joined to the anterior division by a fairly wide isthmus which leads forwards below the processus uncinatus of the crista semicircularis and over the faint ridge formed by the ventrally projecting base of the latter crista. This description of the extensions of the glandula nasalis lateralis furnishes ample proof that the extensions of this gland could hardly be regarded as a criterion for the boundaries of the recessus glandularis. As a matter of fact the recessus glandularis does not seem to be a constant anatomical entity. It certainly has no constant boundaries so that the name "recessus glandularis" could probably be entirely discarded as the area usually alotted to this recess is actually part of the recessus anterior, inferior and supraconchalis.

The pars anterior has a great antero-posterior length. The ventral border of its posterior third is thickened to form the maxillo-turbinal. This turbinal is not in direct continuity with the atrioturbinal anteriorly but is separated from the latter by a wide stretch of deficient paries nasi probably representing an extensive incisura maxillo-atrioturbinalis (VOIT) (fig. 8).

The nasoturbinal is fairly well developed in Suncus. It reaches as far forward as the posterior border of the fenestra superior nasi and it is attached about midway between the upper and lower limits of the pars anterior. The nasoturbinal is continuously fused with the paries nasi, the attachment of its posterior portion causing a very slight sulcus externally. The latter sulcus demarcates the prominentia supraconchalis dorsally (fig. 8). The posterior portion of the nasoturbinal is well developed and projects far downwards into the nasal cavity. Its fusion with the anterior border of the crista semicircularis is only slightly raised and not well defined (fig. 15). Immediately above the incisura Maxillo-atrioturbinalis the nasoturbinal is extremely small and practically disappears, but anterior to this incisura and on the inside of the zona annularis it is again much better defined (fig. 14). The duct of the glandula nasalis lateralis runs forwards directly ventral to the anterior half of the nasoturbinal.

VOL.
28
194

Enclosed between the nasoturbinal and the maxilloturbinal is the well developed recessus supraconchalis which lodges the major anterior part of the glandula nasalis lateralis. Externally this recess gives rise to the prominentia supraconchalis which is perforated near its posterior border by a small elongated fenestra which, however, does not transmit any bloodvessel or nerve (fig. 8).

The atrioturbinal which is usually described as the internal counterpart of the sulcus nasolacrimalis conforms to this description in Suncus although its relations and those of the ductus nasolacrimalis to the zona annularis do not altogether conform to the condition usually prevalent in Mammals. As has already been mentioned the ductus nasolacrimalis enters the nasal cavity behind the lamina transversalis anterior. It again emerges from the nasal cavity through the anterior part of the lamina transversalis anterior and is continued forwards for a short distance in a deep sulcus before re-entering the nasal cavity through the foramen pretransversalis. On its first intranasal passage the nasolacrimal duct is partly enclosed between two cartilaginous ridges, a small ventral and a larger dorsal ridge (fig. 14). These two ridges which together form the atrioturbinal completely surround the nasolacrimal duct in some places and fuse with each other medially to enclose the nasolacrimal duct in a definite canal. Anterior to the exit of the nasolacrimal canal these ridges continued forward and fuse to form the floor of the short sulcus which lodges the anterior part of this canal (figs. 8 and 9). The significance of the above-mentioned condition seems to be obvious. The original sulcus nasolacrimalis which passed across the ventrolateral border of the zona annularis became so deep due to pressure exerted by the nasolacrimal duct that pressure deficiencies were formed at its base. The consequent weakening of the nasal capsule in this region was compensated for by a secondary growth of cartilage over the outer surface of the nasolacrimal duct so that the latter duct was now enclosed inside the newly completed zona annularis. The atrioturbinal and the sulcus lacrimalis therefore still remain homologous with similar structures in other Mammals. The validity of this statement is proved by the development of the nasal capsule in Suncus (see later).

The septum nasi has the shape of a large triangle the base of which is formed by the ventral border of the nasal septum. The apex of the triangle is formed by the anterior limit of the upper border of the subcerebral portion of the nasal septum. From this peak the posterior face of the triangle slopes steeply downwards and backwards almost at right angles to the plane of the slowly declining anterior face of the triangle. The septum nasi, which is widest along its ventral edge, has a great dorso-ventral depth. Its maximum width is found between the cupulae posteriores of the nasal capsule, and directly behind these structures the septum nasi is continued as a solid cylindrical bar. Between the partes anteriores of the nasal capsule the septum

nasi is complete and it does not display a foramen internasale (fenestra septi) as is sometimes found in other Mammals. Immediately anterior to the centre of the combined laminae cribrosae the nasal septum displays a small deficiency about the size of the foramen cribro-ethmoidalis. This deficiency, however, does not transmit any bloodvessel or nerve.

a. *Early development of the Nasal Capsule:* The nasal septum is said to be the first part of the nasal capsule to chondrify. (NOORDENBOS 1904 and 1905 and TERRY 1917). FAWCETT (1921 and 1923) maintains that the septum nasi chondrifies from a separate centre in Tatusia, Xerus and Talpa and that later on it fuses with the posterior division of the central stem. In Suncus the pars trabecularis (including the nasal septum) was found to be blastematously discontinuous with the rest of the central stem in the 6 mm embryo but shortly after this early stage it becomes continous with the remainder of the central stem and seems to chondrify in direct continuity with it. Compared to the rest of the nasal capsule the septum nasi in Suncus is about the first part to chondrify and the chondrification seems to spread from behind forwards. It does not reach the extreme anterior tip of the septum until shortly before the 8.4 mm stage. In the 6 mm embryo the entire nasal capsule is still blastematous. On either side of the blasteme rudiment of the nasal septum three distinct cell concentrations, lying one behind the other, indicate the position of the future cartilagines parieto-tectalis, paranasalis and antorbitalis (TERRY). These cartilages represent the chondrification centra of the tectum and paries nasi. In the 6.8 mm embryo the two first-mentioned pairs of blasteme centres are already fused with the blastematous septum nasi but the posterior centre, which is the smallest of the three, still retains its separate identity. In the 7.2 mm embryo the posterior division of the nasal septum is already sligthly chondrified and in synchondrotic continuity with the pars intermedia (cartilagines paranasales) of the nasal capsule, the latter part being in blastematous continuity with the pars anterior and the pars posterior, both of which are still procartilaginous at this stage. In the 8.4 mm embryo the pars posterior is wholly chondrified and cartilaginously continuous with the rest of the nasal capsule, the pars anterior, however, is only partly chondrified, the latter chondrification comprising the cupulae anteriores and part of the tectum. The lamina transversalis anterior and paries nasi are still densely procartilaginous at this stage and the chondrification of these parts is not completed until after the 9.5 mm stage. From this description it will be observed that although three pairs of blasteme centres could be detected in the nasal capsule, apart from the septum and paraseptal cartilages, chondrification of the tectum and paries nasi spreads from the dorsal border of the septum beginning with the pars intermedia and culminating with the pars anterior. It was interesting to note that the ductus nasolacrimalis in Suncus remain external to the blasteme rudiment of the zona annularis until after the 7.2 mm stage and only then

is it included in the latter by an outgrowth of dense procartilage round its outer surface so that the condition in the adult Suncus has to be regarded as a secondary specialisation.

Concerning the development of the turbinal cartilages it was found that the first to appear in ontogeny are the crista semicircularis and the first primary ethmoturbinal. Both these structures were found to be fairly well developed in the 8.4 mm embryo where traces of the second primary ethmoturbinal, the first and second secondary ethmoturbinals and the nasoturbinal are already to be seen. In the 9.5 mm embryo all the turbinals are developed except for the maxilloturbinal and the third secondary ethmoturbinal.

The cribriform plate does not arise until fairly late end even then appears to grow out from the pars posterior and the pars intermedia of the nasal capsule. The central portion of the cribriform plate is the last to make its appearance.

OL.
28
947

The poorly developed posterior paraseptal cartilage does not chondrify from a separate centre in Suncus but it arises in continuity with the lamina transversalis posterior. Although absent in the later stages a short but well-defined anterior spur to the posterior paraseptal cartilage was found to be present in the 9.5 mm embryo. At this early stage it was already partly invaded by the vomer. This probably accounts for its absence in later developmental stages. The posterior spur to the posterior paraseptal cartilage develops later.

The anterior paraseptal cartilage does not chondrify until fairly late. Even as early as the 6 mm stage the position of the future anterior paraseptal cartilage could be distinguished as an isolated concentration of cells free from both the nasal septum and the lamnia transversalis anterior. In the 8.4 mm embryo the anterior paraseptal is still densely procartilaginous but at this stage it is blastematously continuous with the lamina transversalis anterior. In the 9.5 mm embryo the anterior paraseptal cartilage was found to be fairly well chondrified, and in very slight synchondrotic continuity with the lamina transversalis anterior. There cannot, however, be any doubt that the anterior paraseptal cartilage in Suncus arises from an autogenous chondrification centre as in the cat (Terry 1917), pig (Sturm 1937), hedgehog (see Sturm 1937) and horse (Arnold 1928). The recurved ventral edge of the vertical lamella of the anterior paraseptal cartilage which is still procartilaginous in the 9.5 mm embryo is the last part of the anterior paraseptal to chondrify. In the 15.6 mm stage it is already complete and its anterodorsal end is attached to the dorsolateral border of the vertical lamella by a delicate vertically placed "outer bar". This latter structure, however, is resorbed soon after its formation. It will be recalled that in the 18.3 mm stage only a band of connective tissue marks the position of the "outer bar". The occurrence of the "outer bar", as far as its development and resorption is concerned, is subjected to considerable variation in the groups of Mammals in which it has been described. So for instance we

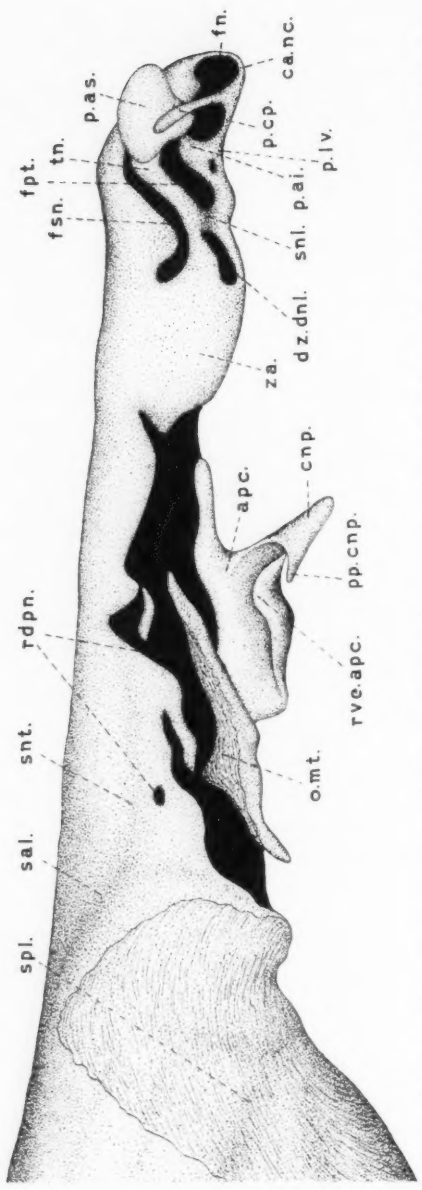

Fig. 23. Lateral view reconstruction of the nasal capsule—pars respiratoria—of a 25.5 mm embryo—indicating the position and extent of ossification centres present at that stage (× 22).

find that ARNBÄCK CHRISTIE LINDE (1914) maintains that the "outer bar" becomes reduced in older embryos, while as is the case in Suncus, it may be formed fairly late and be resorbed again very soon after its formation. On the other hand it may be formed very late and be retained in its complete form in the adult as in Erinaceus (MICHELSSON 1922 and SPURGAT 1896) and the pig (STURM 1937).

As regards the significance of the "outer bar" different opinions are held. BROOM, who first described and named this structure in Macroscelides (1896), as well as ARNBÄCK CHRISTIE LINDE (1914) regard it as a primitive structure and homologize this structure in the Marsupials and Placentals with a turbinal which is still present in the Monotremes. TOEPLITZ (1920) strongly opposes this homology, and maintains that the "outer bar" "ist nichts als eine überdachung der Mündungstelle des Canalis Nasopalatinus, eine Restpange gewissermassen der Seitenwand des Paraseptalknorpels wie sie gerade an dieser stelle bei einer ganzen Reihe auch placentaler Säugetiere auftritt." DU TOIT (1942) gives a list of Mammals in which an "outer bar" in lowly orders of Mammals has been described. BROOM (1939, p. 325) writes: "An outer bar is a Marsupial character which is retained in the Edentata, the Tubulidentata, the Menotyphla and the Chrysochloridae." Apart from these we may also find an "outer bar" in higher Mammals viz; in some of the Lipotyphla: Erinaceus, Suncus, Sorex and Crocidura, also in the pig and ox (STURM 1937). This latter author (p. 208) concludes: "Diese Tatsache, dass der Knorpel bei hochentwickelten Säugern noch in späten Embryonalstadien eine erhebliche Vervollkomnung erfährt und dann auch beim Erwachsenen in vollen Umfange erhalten bleibt, spricht jederfalls nicht dafür, dass wir es mit einem Seitenwandrudiment zu tun haben, sondern weist vielmehr auf eine progressive Bildung hin." DU TOIT (1942) also remained sceptical regarding the taxonomic value of the nasal cartilages.

The cartilago ductus nasopalatini in Suncus is formed even later in ontogeny than the anterior paraseptal cartilage. In the 8.4 mm embryo only a slight blasteme trace of the proximal division of the nasopalatine cartilage was encountered and it was found to be continuous with the antero-ventral aspect of the anterior paraseptal cartilage. In the 9.5 mm embryo the nasopalatine cartilage is clearly outlined in procartilage, slight chondrification spreading from the anterior paraseptal cartilage has already set in at its proximal division. Chondrification of this structure is nearly complete in the 15.6 mm embryo. Its posteriorly directed spur (cartilago palatini), however, does not arise from an autogenous centre and although fairly small at this stage it rapidly increases in size in later development.

b. *Post optimal changes in the nasal capsule:* (figs. 11 and 23—26). The post optimal changes in the nasal capsule can be summed up under two heads: a,—resorption and b,—ossification.

The resorption of cartilage in the solum nasi is rather limited. It affects mainly the anterior process of the anterior paraseptal cartilage. This process, although extremely thin, is still in contact with the lamina transversalis anterior in the 22 mm embryo, but shortly after this stage it is resorbed from its anterior end. In a juvenile specimen of Suncus measuring 28 mm only a short stump of this anterior process is left (fig. 25). The rest of the anterior paraseptal cartilage is retained in its complete form in the adult. Except for the anterior process of the cartilago paraseptalis anterior the only other part of the solumn nasi which is affected by resorption is the vertical medial lamella of the lamina transversalis anterior. This lamella is resorbed from its posterior end in confluency with the extensive basal fenestra; thus resulting in the formation of a deep incisura which partly separates the lamina transversalis anterior from the nasal septum (figs. 12 and 24). In the 28 mm specimen of Suncus the anterior end of the lamina transversalis anterior is still fused with the nasal septum so that the zona annularis is not completely obliterated even at this stage.

In the tectum and paries nasi more extensive resorption is encountered than in the solum nasi. The processus alaris superior loses direct contact with the processus lateralis ventralis in the 25.5 mm stage, remaining only in extremely slight cartilaginous continuity with the paries nasi ventral to the fenestra superius nasi (fig. 23). This latter fenestra is also expanded forwards into the roof of the cupula anterior. The latter resorption of cartilage, however, does not take place until fairly late and is not pronounced until in the 28 mm stage. In the paries nasi of the pars anterior the main resorption centre is in the prominentia supraconchalis. As a matter of fact already in the 18.3 mm embryo a small fenestra of seemingly no significance has been reported in this prominence (fig. 8).

The resorption of the cartilaginous nasal wall in this region results in the detachment of the maxilloturbinal; a process which is nearly completed in the 22 mm embryo. In the 25.5 mm stage the maxilloturbinal is entirely free and opposite its anterior end the resorption of the cartilage spreads upwards to form a deep incisura in the paries nasi (fig. 11). This process is continued in the later stages until in the juvenile Suncus the resorption has spread across the tectum nasi and upper edge of the septum to establish continuity with the resorption spreading from the opposite side (figs. 24—26). As a result of this resorption the anterior ends of the nasoturbinals become detached from their greater posterior portions (plate XIII).

Apart from the resorption centre in the prominentia supraconchalis, another important centre appears in the tectum nasi slightly behind the zona annularis and postero-dorsal to the incisura maxilloatrioturbinalis. This resorption centre which is clearly defined in the 25.5 mm stage spreads forwards and medialwards establishing continuity with the resorption from the opposite side (figs.

VOL
28
194

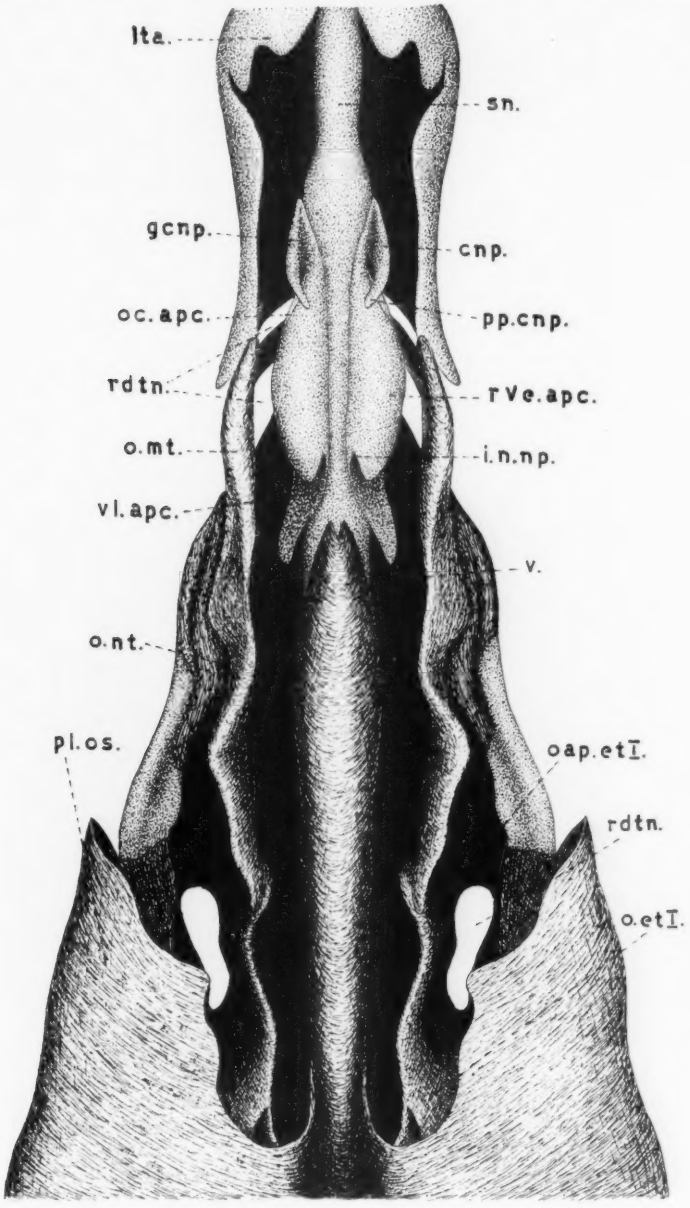

Fig. 24. Ventral view reconstruction of the middle portion of the nasal capsule of a 28 mm embryo (× 30).

25 and 26). It also gains continuity with an extensive deficiency in the upper part of the nasal septum antero-ventral to this region. This latter deficiency does not appear until after the 25.5 mm stage but even in the 22 mm embryo

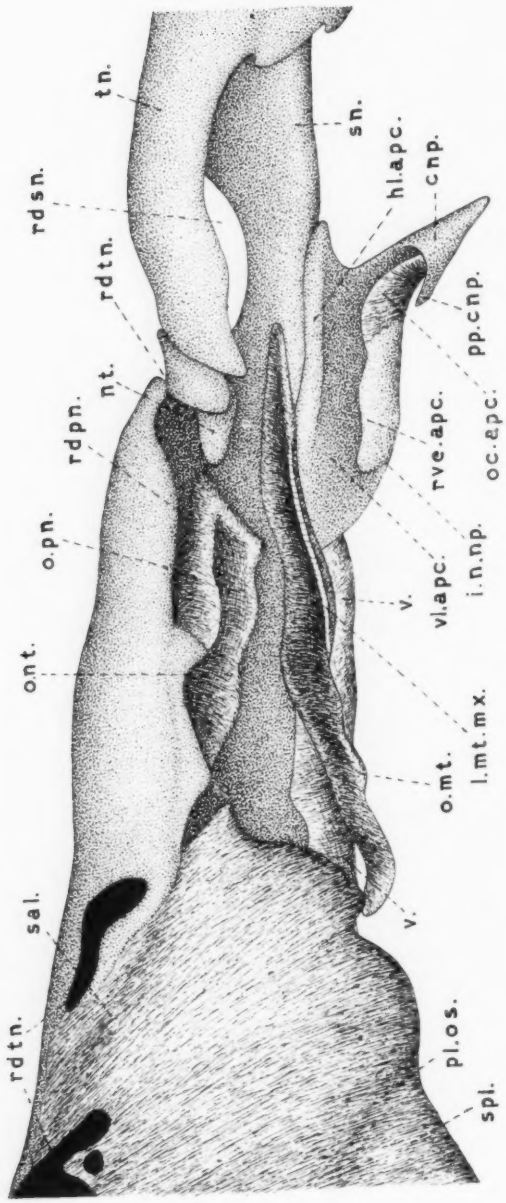

Fig. 25. Lateral view reconstruction of the middle portion of the nasal capsule of a 28 mm embryo (× 30).

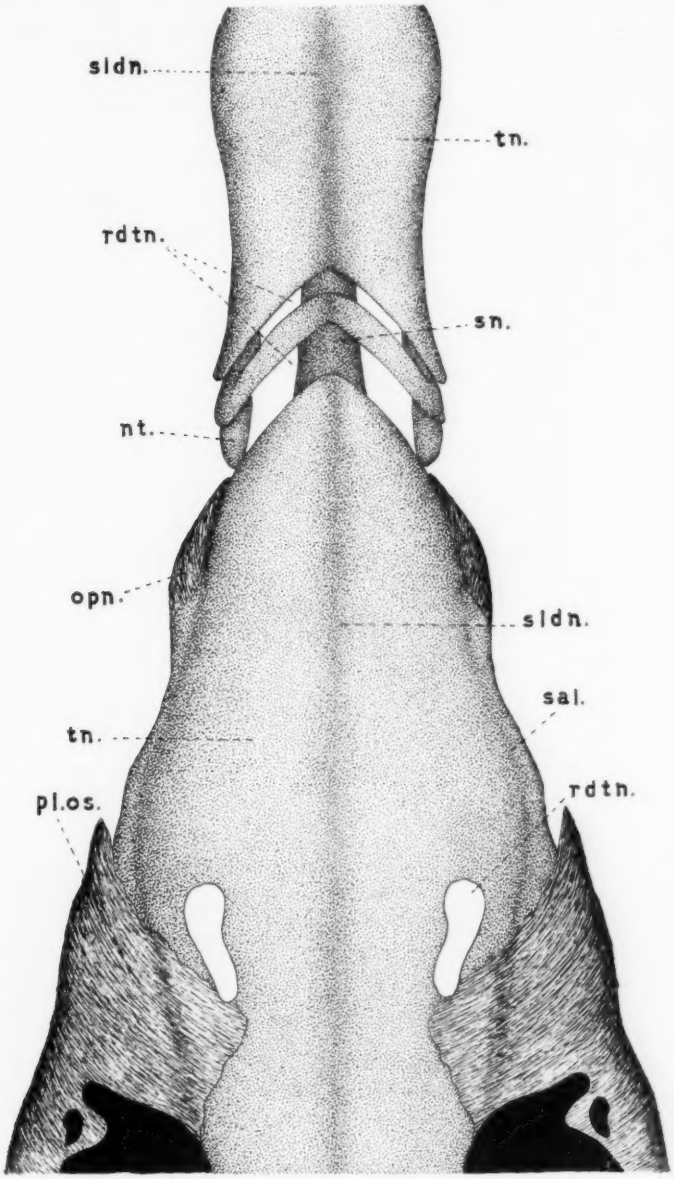

Fig. 26. Dorsal view reconstruction of the middle portion of the nasal capsule of a 28 mm embryo(× 30).

a marked thinning of the nasal septum in this region can be detected. Simultaneous with the thinning and resorption of the upper part of the nasal septum the ventral edge of the septum in the same region gains considerable thickness

until eventually it takes the form of a cylindrical rod ventral to the deficiency. BROOM (1915 b) reported a somewhat similar condition in an adult Centetes.

Between the two resorption centres in the tectum and paries nasi just mentioned a slender transverse rod of cartilage is retained. This rod is not directly continuous with the rest of the nasal capsule but it completely separates the two resorption centres previously described, and the anterior detached portions of the nasoturbinals remain attached to its anterior ventro-medial edges (figs. 25 and 26). As a result of this resorption in the tectum, septum and paries nasi immediately anterior to the dermal bone roof of the nasal capsule the anterior division of the pars anterior becomes detached from the greater posterior division of the nasal capsule except for the cylindrical ventral edge of the nasal septum which remains intact. The reason for this resorption is obvious as the region behind the zona annularis where only the cylindrical septum remains intact undouptedly forms the base on which the proboscis can carry out its rotatory movements which are so often preceived in the living shrew.

In the juvenile Suncus, immediately before ossification sets in, extensive resorption from different centres renders the paries and tectum nasi in the pars intermedia and pars posterior well fenestrated. This resorption especially affects the prominences caused by the internal recesses between the ethmoturbinals but all these resulting fenestrae are completely roofed over by the frontals.

Ossification in the nasal capsule emanates from different centres. Up to the 28 mm stage the only part of the anterior paraseptal cartilage to ossify is the anterior end of the recurved vertical lamella which corresponds with the postero-ventral root of the "outer bar" (fig. 25). This ossification does not commence until late, being non-existent in the 25.5 mm stage.

In the regio respiratoria of the nasal capsule both the maxilloturbinal and the nasoturbinal ossify from autogenous centres (figs. 24—26). The first trace of ossification in the maxilloturbinal has been noticed at about the centre of the latter structure in the 22 mm embryo. In the juvenile Suncus of 28 mm the entire maxilloturbinal is ossified and its ventro-lateral edge is fused for a short distance with the inner aspect of the maxilla, a condition not uncommon amongst Mammals. As compared to the maxilloturbinal the nasoturbinal ossifies fairly late. In the 25.5 mm stage an ossification centre in the most prominent part of the latter structure could be distinguished. In the 28 mm stage this ossification centre is still clearly separated from the ethmoid bone, and neither does the ossification at this stage invade the extreme anterior end of the nasoturbinal.

In the posterior Regio olfactoria of the nasal capsule the extensive ethmoid bone ossifies from three main centres, Although several minor centres of ossification may be present. The medial septal portion of the ethmoid (pars perpendicularis of the mesethmoid) ossifies from an autogenous centre which

VOL
28
194

can be clearly distinguished in the 22 mm stage of Suncus. From this centre the ossification spreads into the crista galli and cribriform plates so that the latter plates do not ossify in continuity with the lateral pleurethmoids. In the young specimen of Suncus (25.5 mm) the major part of the cribriform plates is ossified but is still entirely separated from the pleurethmoids. In the 28 mm stage the mesethmoid is already fused with the pleurethmoids laterally and its pars perpendicularis is well developed although the extreme ventral edge of the nasal septum in this region remains cartilaginous. Postero-ventrally the mesethmoid is fused with the orbitosphenoid. It extends backwards as far as the cupulae posteriores of the nasal capsule where it functionally replaces the anterior end of the poorly developed presphenoid. It may be recalled from a previous chapter that the presphenoid has no separate osseous identity in Suncus but that it ossifies in continuity with the orbitosphenoids.

The lateral pleurethmoids in Suncus make their first appearance at a very early stage. In the 18.3 mm embryo a definite ossification centre could already be distinguished in the antero-ventral aspect of the anteriorly directed spur of the first primary ethmoturbinal (figs. 9 and 20). This ossification centre proved to be the main centre of the pleurethmoid, and from here the ossification was found to spread rapidly into the surrounding regions of the nasal capsule. In the 18.3 mm embryo another small ossification centre could be distinguished in the uncinate process and the adjoining free edge of the crista semicircularis (fig. 15). Ossification, spreading from this centre, gains continuity with the ossification spreading from the first primary ethmoturbinal before the 25.5 mm stage. Similarly the third primary ethmoturbinal displays a separate ossification centre in the 22 mm stage. This centre, however, very soon fuses with the surrounding ossified parts. In the 22 mm embryo continuity is already established between the pleurethmoid and the lateral lamella of the vomer, which invades the posterior paraseptal cartilage and the lamina transversalis posterior.

C. THE DORSAL STRUCTURES.

The orbitoparietal and sphenethmoid commissures and the parietal plates have been dealt with before.

The supraoccipital cartilages are joined in the mid-dorsal line to form the tectum posterius which delimits the foramen magnum postero-dorsally. Antero-ventrally the supraoccipital is fused with the exoccipital of the corresponding side; antero-dorsally it is fused with the parietal plate. The supraoccipital cartilage is separated from the otic capsule by the fissura occipito-capsularis superior. This fissure is bridged over towards its middle by an inconspicuous antero-ventrally directed outgrowth (processus opercularis of FAWCETT) which has been previously described (fig. 3).

Due to the lack of the critical intermediate stages I was unable to determine the earliest development of the supraoccipital cartilages which occurs somewhere between the 7.2 and 8.4 mm stages in Suncus.

As far as could be discerned in Suncus the supraoccipital ossifies from a single centre which is well developed in the 9.5 mm embryo, but which, at this stage, occupies merely the anterior and antero-medial edges of the supra-occipital cartilages. It is possible, however, that the supraoccipital may have arisen from two ossification centres as is usually the case but that these centres have become fused with each other soon after their formation. The supra-occipital ossification fuses with the exoccipital ossifications shortly after birth and it also acquires continuity with the interparietal plate.

IV. THE DERMAL BONES.

For a description of the dermal bones an 18.3 mm embryo of Suncus has been chosen.

A. THE PREMAXILLA

in the 18.3 mm embryo consists of a well defined alveolar portion and a strongly developed processus extranasalis. This latter process bears a long posteriorly directed spur which partly overlaps the ventral border of the nasal (fig. 18). Clamped between this spur of the processus extranasalis and the posterior alveolar portion of the premaxilla is the anterior end of the frontal process of the maxilla. The palatine process of the premaxilla is well developed and it projects medialwards in front of the ductus nasopalatinus. Attached to the postero-medial end of the processus palatinus is a strongly developed and posteriorly directed processus prevomeralis. This process has the shape of a broad vertically placed bony plate closely applied to the medial aspect of the vertical lamella of the anterior paraseptal cartilage. Attached to the dorso-medial aspect of the latter cartilage is a slight cartilaginous shelf which projects medialwards over the upper edge of the processus palatinus medialis so that the latter process functions as an efficient support for the anterior paraseptal cartilage (fig. 17). The posterior end of the processus palatinus medialis is situated dorsal to the anterior end of the palatine process of the maxilla and it ends just in front of the anterior border of the vomer. Enclosed between the palatine processes of the premaxilla and the maxilla is the foramen incisivum through which the nasopalatine duct and Stenson's duct from Jacobson's organ communicate with the buccal cavity. The nasopalatine nerve also passes through the posterior corner of this foramen.

During the later stages of development the palatine processes of the premaxillae completely fuse with each other in the mid-line. Similarly the pos-

teriorly directed processus palatinae mediales of the two premaxillae fuse with each other.

Concerning the early development of the premaxilla it was found that the first part of the premaxilla to appear is the anterior junctional region between the palatine process and the dental or alveolar portion. This part of the premaxilla is already slightly ossified in the 7.2 mm embryo of Suncus. The ossification of the entire premaxilla, even of the processus palatinus medialis, spreads from this centre so that the latter process has no separate ontogenetic identity as is the case in many other Mammals (see DE BEER 1929).

The homology of the processus palatinus medialis in Mammals has been a topic of much controversy in the past. For a detailed review of the opinions held by various authors, viz. GAUPP, FUCHS, BROOM, WILSON, PARKER and others on this point the reader is referred to DE BEER (1929) and STADTMÜLLER (1936). Judging from the condition prevalent in Suncus, however, one certainly has to appreciate BROOM's views expressed as follows: "it seems much more satisfactory to regard it (i.e. the proc. palatinus medialis) as a true portion of the premaxilla which has replaced an anterior vomerine element such as the dumb-bell bone of Ornithorhyncus, than to regard it as the homologue of that bone." (BROOM 1902 a).

OL.
28
947

B. THE MAXILLA

in Suncus is large and consists of the usual parts viz. a wide backwards directed frontal process which laterally covers the prominentia supraconchalis, the prominentia inferior and the prominentia anterior (fig. 20). This process joins the premaxilla, nasal, frontal and lacrimal. Furthermore the maxilla has a massive alveolar portion from the postero-lateral corner of which a small zygomatic process projects backwards and sideways to end in a free pointed extremity. Between the frontal and alveolar portions of the maxilla the large infraorbital foramen transmits the maxillary branch of the trigeminal nerve. This foramen is deliminated postero-dorsally by the lacrimal bone, which in this region is wedged between the frontal and alveolar portions of the maxilla. The horizontal medially directed palatine process of the maxilla forms part of the secondary hard palate. It floors the extensive basal fenestra in the nasal capsule and forms a support for the posterior end of the anterior paraseptal cartilage. The palatine process of the maxilla is pierced by a foramen for the transmission of the major palatine nerve. Along its medial edge this process of the maxilla displays a conspicuous nodule of secondary cartilage.

During the later stages of development in Suncus the palatine processes of the maxillae become completely fused. Similarly the lacrimal bone, which forms the posterior border of the infraorbital foramen, becomes completely fused with the alveolar portion of the maxilla below, and with the frontal process

of the maxilla above. After having pierced the lacrimal bone the nasolacrimal duct runs through a canal in the maxilla for a considerable distance before it emerges on the medial aspect of this bone relatively far forwards.

The maxilla ossifies from a single centre in its future alveolar portion. The first indication of ossification was found in a 7.2 mm embryo.

C. THE LACRIMAL BONE

is fairly well developed and in the 18.3 mm embryo it is entirely exposed on the side of the skull. It occupies the anterior corner of the orbit. The thickened anterior end of the lacrimal is pierced by the nasolacrimal canal. As previously stated the lacrimal bone in Suncus becomes inseparably fused with the maxilla during the later stages of development.

Compared to the maxilla and premaxilla the lacrimal bone develops fairly late. It ossifies from a single centre around the nasolacrimal canal and first appears in the 9.5 mm embryo.

D. THE JUGAL (ZYGOMATICUM OR MALARE)

was found to be entirely absent in Suncus so that a wide gap results between the short zygomatic processes of the maxilla and squamosum. This is not an exceptional condition as the absence of a jugal, exclusive of the Insectivores, has also been reported in Echidna, while it is rudimentary in Ornithorhynchus, Manis and the Myrmecophaga. Regarding the relations of the jugal in Insectivores WEBER (1928, p. 97) states: "Bei allen übrigen Insectivora (i.e. exclusive of the Tupiidae and the Macroscelidae) vereinigt sich Orbita und Temporalgrube vollständig und ist der Jochbogen schwach oder es fehlt wie bei Centetidae, Solenodontidae und Soricidae. Dementsprechend fehlt das Jugale, dessen Rudiment wohl mit dem Processus zygomaticus des Maxillare verschmilzt. Bei Sorex sacralis fand PETERS es wenigstens diesem noch aufsitzend." FAWCETT (1918 a) reports the presence of a small but free jugal in the adult skull of Erinaceus europaeus. In Suncus, as has been stated previously, the zygomatic process of the maxilla ossifies in continuity with the rest of the maxilla, so that here at least, no rudiment of the jugal is left. HOGBEN (1919), commenting on the progressive reduction of the jugal in Mammals speaks of the "general tendency among the Mammals for the displacement of the jugal without apparent reference to function at all" (p. 73).

E. THE PALATINE.

The laminae horizontales (v. palatinae) of the palatines in the 18.3 mm embryo of Suncus are completely fused in the middle line (fig. 20). Together

they form the posterior division of the secondary palate and as such represent a backward continuation of the palatine process of the maxillae. The anterior border of the apertura nasalis interna is formed by the posterior edge of the fused horizontal laminae of the palatines. The palatine portion of the hard palate is pierced by two pairs of foramina for the transmission of the medial palatine nerves. The posterior lamina verticalis or pars perpendicularis of the palatine forms a trough-shaped covering for the ventral surface of the lamina transversalis posterior. The medial wall of this trough is the higher of the two and it practically reaches the vomer dorso-medially thus forming the lateral wall to the ductus nasopharyngeus (fig. 22). Postero-laterally the palatine nearly reaches the alisphenoid. This posterior division of the palatine forms the floor of the anterior portion of the cavum epiterycum and it supports the anterior extremity of the Gasserian ganglion. The pterygoid bone is closely applied to the postero-ventral aspect of the palatine.

VOL. 28 1947

The relations of the palatine to the neighbouring structures remain more or less the same during the later stages of its development.

The two palatines in Suncus ossify separately, each from a single centre which can be distinguished in the 8.4 mm embryo. This ossification centre of the palatine is at about the junctional point of the horizontal and vertical laminae of the bone. Fusion of the two horizontal laminae of the palatines does not take place until after the 9.5 mm stage. In the 15.6 mm embryo the horizontal laminae of the palatines were found to be completely fused with minute nodules of secondary cartilage scattered about in the line of fusion.

F. THE VOMER

is a large unpaired dermal bone. It is trough-shaped and invests the ventral edge of the septum nasi (fig. 20). The anterior end of the vomer begins directly behind the processus palatinae mediales of the premaxillae and is situated between the two anterior paraseptal cartilages in this region (fig. 18). Further back and just in front of the palatines the trough-shaped vomer gains considerably in depth, its ventral edge being partly wedged between the palatine processes of the maxillae (fig. 19). Directly anterior to the origin of the ductus pharyngeus the dorso-lateral edges of the vomer curve downwards forming two additional limbs so that in section the vomer in this region appears M-shaped (fig. 21). These lateral limbs of the vomer invade the anterior edges of the lamina transversalis posterior and the posterior paraseptal cartilages. In the 18.3 mm embryo this invasion affects only the anterior and medial portions of the posterior paraseptal cartilage. In later stages, however, the invasion is carried still further and it affects the entire posterior paraseptal cartilage including the posterior spur of the latter. The posterior end of the

vomer is shaped like a shallow trough which does not extend quite as far back as the posterior ends of the palatines (fig. 22).

In the adult Suncus the posterior division of the vomer is inseparably fused with the ethmoid bone (fig. 25). The relations of its vertical lateral lamellae with the laminae perpendiculares of the palatines are also very intimate in the adult.

Regarding the development of the vomer in Mammals STADTMÜLLER (1936, p. 934) says: "Er (the vomer) ist ein unpaares, aber ontogenetisch meist aus zwei Hälften verschmolzenes Element, dass nicht mehr horizontal wie bei den meisten Reptilien sondern vertikal liegt." In Suncus the vomer was first observed in the 9.5 mm embryo. At this stage the two halves are already fused in several places, but a series of deficiensies in the middle line suggest the separate origin of the two halves. I was unable to confirm this beyond doubt as the younger stage which I had at my disposal, an 8.4 mm embryo, showed no signs of ossification in this region. In the 9.5 mm stage the dorso-lateral edges of the vomer already invade the anterior spurs of the posterior paraseptal cartilages, so that this latter part of the vomer and especially the later lateral limbs of the vomer undoubtedly have a mixed character. FAWCETT (1911) described an invasion of the anterior paraseptal cartilages by the vomer in the human. FUCHS (1909) and ZUCKERKANDL (1908) described similar conditions in the cat, the latter author maintaining that the posterior paraseptal cartilage in the cat is also invaded by the vomer. This was probably the case at a fairly late stage.

VOL
28
194

G. THE PTERYGOID

is well developed. There are not, however, two pairs of elements as is the case in the Menotremes and in several other Mammals (see DE BEER and FELL 1936, p. 22). The anterior portion of the pterygoid is closely applied to the ventral surface of the posterior portion of the palatine. In about the region where the palatine disappears from vertical sections the pterygoid bears a thick process directed downwards and backwards. This process or hamulus is situated ventro-lateral to the ductus nasopharyngeus and it partly supports the soft palate. The tendon of the tensor palati muscle hooks round the base of the hamulus before being inserted into the soft palate. Behind the hamulus the pterygoid is continued backwards as a wide trough which takes part in the formation of the floor of the cavum epiterycum and lodges the anterior portion of the Gasserian ganglion (fig. 4).

The medial wall of this trough forms part of the lateral wall of the ductus nasopharyngeus. The postero-lateral end of the pterygoid bone invades the medial edge of the pterygoid process of the ala temporalis for a short distance. In the adult Suncus the posterior end of the pterygoid is inseparably fused with

the postero-medial edge of the alisphenoid while its relations with the basisphenoid are also very intimate. This posterior end of the pterygoid forms a roof over the pharyngeal end of the Eustachian tube and forms the anterior border to the canalis Vidianus for the transmission of the Vidian nerve and a large vein.

In the 9.5 mm embryo the greater anterior part of the pterygoid is cartilaginous. This cartilaginous portion (pterygoid cartilage) bears a small postero-ventrally directed spur, which, when it becomes ossified later on, forms the ventral spur or hamulus of the pterygoid. The posterior end of the pterygoid in the 23.5 mm embryo is ossified and it has the character of a true dermal bone which already at this early stage invades the medial edge of the processus pterygoideus (fig. 11).

The first indication of a pterygiod ossification in Suncus was encountered in the 8.4 mm embryo where an extremely slight ossification centre could be detected at about the junctional point between the osseous and cartilaginous portions of the pterygoid as figured for the 9.5 mm embryo. From this centre the ossification spreads backwards in true dermal bone fashion while the centre expands forwards by the formation of a fairly extensive pterygoid cartilage. This latter cartilage has no separate origin but in the 8.4 mm embryo its blasteme rudiment is inseparably fused with the already mentioned ossification centre.

VOL. 28 1947

H. THE NASAL

presents little of particular interest. In the 18.3 mm embryo of Suncus the nasal extends forward to about as far as the posterior third of the anterior paraseptal cartilage and as far back as the posterior limit of the precerebral portion of the tectum nasi. The two nasals are fused with each other in the mid-dorsal line for about the posterior two-thirds of their length. Each nasal establishes relations with the extra nasal process of the premaxilla, with the frontal process of the maxilla and with the frontal bone itself. The junction between the nasals and frontals is roughly chevron-shaped with the apex directed backwards in much the same way as in the Carnivores and Lemuroidea.

In the adult Suncus the nasals are strongly developed and not pneumatic. They reach forward as far as the posterior border of the deficient area in the tectum and paries nasi so that the nasals do not interfere with the mobility of the proboscis.

Each nasal in Suncus ossifies from a single centre shortly after the 8.4 mm stage. In the 9.5 mm embryo the nasals were found to be very small and still quite separate.

I. THE FRONTALS

in the 18.3 mm embryo of Suncus are fairly extensive and form a suture in the mid-dorsal line. They overlie the hindermost part of the nasal capsule dorso-laterally and are also closely applied to the commissura sphenethmoidalis and the als orbitalis. Each frontal bears relations to the nasal, parietal, lacrimal and maxilla. After the posterior part of the nasal capsule has become ossified the frontals bear close relations with the ethmoid ossification and completely roof over the numerous deficiencies caused by the resorption in the dorsal and dorso-lateral aspects of the latter ossification. In several places, especially at the roots of the turbinals, the ethmoid may be in slight synostotic continuity with the frontals. Posteriorly the frontals fuse with the parietals during the later stages of development.

The frontal in Suncus first appears as an ossification in the 8.4 mm embryo where it has the form of an extremely thin bony plate lying dorso-lateral to the commissura sphenethmoidalis.

VOL. 28 194

J. THE PARIETALS

are extensive bony plates which, in the 18.3 mm embryo of Suncus, do not meet in the mid-dorsal line. The bulk of each parietal extends backwards from the posterior extension of the ala orbitalis and forms a lateral and dorso-lateral protection for the brain. In the otic region the parietal overlaps the parietal plate of the chondrocranium laterally and extends as far down as the prominentia semicircularis superior (anterior). Furthermore, each parietal sends a long ventro-lateral process forward which overlaps the frontal ventro-laterally and extends as far forward as the postero-lateral aspect of the nasal capsule. This process completely separates the squamosal from the frontal. During the later stages of development this anterior process of the parietal becomes inseparably fused with the anterior upper edge of the squamosal and also with the frontal. The major posterior part of the periotic (pars mastoidea) remains uncovered by the parietal. The parietals do not fuse with the interparietal and the junctional region between the posterior ends of the two parietals and the interparietal is the last part of the roof of the brain capsule to ossify.

As far as could be determined from the embryonic material at my disposal the parietal in Suncus ossifies from a single centre which is already clearly visible in the 7.2 mm embryo. At this stage the parietal can be distinguished as an extremely thin bony plate which lies lateral to the brain in the wide gap between the future ala orbitalis and the parietal plate. It is, however, quite possible that the anteriorly directed process of the parietal ossifies from a separate centre as its connections with the greater posterior division of the parietal

is only slight in the 15.6 mm embryo. In the younger stage viz. a 9.5 mm embryo, this latter process of the parietal is not yet present.

K. THE SQUAMOSAL

in Suncus is a well developed dermal bone with a well defined processus postglenoideus and a glenoid fossa for the articulation of the dentary. It does not, however, show any indication of a zygomatic process so that the squamosal does not take any part in the formation of the deficient zygomatic arch. What is left of the latter arch consists merely of a short maxillary zygomatic process. The posterior squamous or temporal portion of the squamosal is broad and plate-like. It plays an important part in the formation of the ventro-lateral portion of the brain capsule. The posterior extension of the squamosal lies lateral to the otic capsule and extends as far back as the primary stylo-mastoid foramen.

During the later stages of development the anterior lower edge of the squamosal becomes completely fused with the upper outer edge of the ali-sphenoid, the latter of which takes part in the formation of the postero-ventral shelf of the glenoid fossa. The anterior upper border of the squamosal in the later stages also becomes inseparably fused with the antero-ventral border of the parietal. The posterior end of the squamosal, however, remains free from the parietal and a large portion of the periotic remains exposed between the posterior end of the squamosal and the lower edge of the parietal.

The first part of the squamosal to ossify is the processus postglenoideus. This ossification centre makes its appearance in the 20 mm embryo. In the 9.5 mm embryo the processus postglenoideus is still the only part of the squamosal to ossify, so that the squamous portion does not develop until fairly late.

L. THE TYMPANIC (ECTOTYMPANIC)

bone in the 18.3 mm embryo of Suncus forms about three quarters of a circle and surrounds the tympanic membrane anteriorly, medially and postero-medially so that the deficiency in the tympanic bone is directed backwards, upwards and sideways. The lateral division of the antero-dorsal limb of the tympanic bone is fairly closely applied to the ventral surface of Meckel's cartilage and the gonial. It bears a short anteriorly directed spur which follows the anterior extension of Meckel's cartilage for a short distance. The tympanic bone retains this characteristic horseshoe shape throughout life and does not form a tympanic bulla during the later stages of its development; neither does it acquire any intimate relations with the processus tympanicus petrosi caudalis. This condition of the tympanic bone in Suncus has to be regarded as primitive and it coincides with the condition prevalent in several

other groups of Mammals viz. Monotremes, Didelphidae, many Insectivores, Chiroptera and Xenarthra as well as in Orycteropus, Sirenia, Lemuroidae and Chiromyidae.

The tympanic bone in Suncus ossifies from a single centre situated in its anteromedial part. This ossification centre could first be observed in the 9.5 mm embryo at which stage it was already fairly extensive.

M. THE GONIAL (PREARTICULAR)

in Suncus is a small spicule of bone the anterior part of which has the shape of a shallow horizontal through applied to the ventral surface of the posterior division of Meckel's cartilage. The upper limb of the tympanic bone is closely applied to the ventral surface of the gonial in this region. The chorda tympani nerve comes to lie between the gonila and Meckel's cartilage and eventually pierces the former on its course downwards. Posterior to the foramen for the chorda tympani the gonial loses its horizontal character and changes to a vertical bony plate which invades Meckel's cartilage in the notch between the manubrium and caput mallei to form the adult "processus Folii", or "anterior process of the manubrium". After the resorption of Meckel's cartilage in the juvenile Suncus the anterior tip of the gonial (processus Folii) remains attached by means of a fairly strong ligament to the thin spicule of bone which ossifies in Meckel's cartilage ventral to the posterior end of the dentary.

The gonial makes its appearance in the 9.5 mm embryo of Suncus as a minute splint of bone ventral to the posterior portion of Meckel's cartilage and it has a true dermal bone character.

N. THE INTERPARIETAL

in Suncus is a fairly extensive bone lying in the mid-dorsal line in front of the supraoccipital. It ossifies relatively late, being absent in the 9.5 mm embryo. Soon after its formation it fuses with the supraoccipital. It does not, however, fuse with the parietals at any stage of its development.

V. SUMMARY.

The following points in the development of the chondrocranium and early osteocranium of Suncus are noteworthy:

a. *The central stem.*

1. The central stem is almost straight not being acutely bent in the region of the cella turcica.

VOL
28
194

2. No fenestra hypophyseos is retained at the optimal stage of chondrification.
3. The alicochlear commissures are well defined.
4. The fossa hypophyseos is bearly visible due to the absense of a dorsum sellae.
5. The different regions of the central stem become confluent at a very early stage of their development.
6. The planum basale shows no indication of either a fenestra basicranialis posterior or paired parachordals at any stage of its development.
7. The fissura basicochlearis develops fairly late.
8. The notochord is of the primitive retrobasilar type (Tourneux) and is resorbed again in early ontogeny.
9. The "polar elements" in the lamina hypophyseos develop early in ontogeny but the alicochlear commissures appear fairly late.
10. It is concluded that the alicochlear commissure probably represents a delayed rudiment of the postero-lateral wall of the trabecula, which, in some Mammals may be entirely absent.
11. Only three ossification centres could be distinguished in the central stem: viz. basioccipital, basisphenoid and mesethmoid. The presphenoid ossification centres are absent.
12. The basioccipital appears first and the mesethmoid last.

b. *Exoccipital cartilages.*

1. Only one pair of hypoglossal foramina is present.
2. The lamina alaris is well developed and fused with the commissura occipito-capsularis posterior, thus obliterating the fissura occipito-capsularis inferior.
3. The exoccipital cartilage seems to chondrify in continuity with the planum basale.
4. The lamina alaris of the exoccipital develops fairly late in ontogeny.
5. The exoccipital bone ossifies from one main centre but a small accessory centre appears in the processus paracondyloideus.
6. The occipital condyle is formed mainly by the exoccipital but the basioccipital also partakes in the formation of its antero-ventral tip.

c. *Auditory capsule.*

1. A large basicochlear fissure is present but it is subdivided into an anterior and posterior division by means of a wide anterior chordo-cochlear commissure.
2. The apertura medialis of the recessus scala tympani is delimited from the foramen jugulare.
3. No fissura occipito-capsularis inferior is present but the fissura occipito capsularis superior is well defined.

4. The parietal plate is well developed and connected with the supraoccipital and otic capsule but not with the ala orbitalis.
5. The opercular process is well developed.
6. A foramen faciale secundarium is present.
7. O shallow fossa subarcuata inferior interna is present
8. The recessus supra-alaris is extensive.
9. The processus paracondyloideus is well developed.
10. A well defined processus tympanicus petrosi caudalis is present.
11. No rostral or caudal entotympanic cartilages could be distinguished.
12. A separate foramen singulare is absent.
13. In the foramen acusticum inferius a small foramen for the lower nerve to the saccule is isolated.
14. The foramen endolymphaticum is extensive and displays rather complicated relations.
15. The fenestra ovalis and rotunda display normal relations.
16. The apical portion of the septum spirale is poorly developed.
17. The otic capsule chondrifies from two main centres—one in the pars canalicularis and the other in the floor of the pars cochlearis.
18. The parietal plate chondrifies from an autogenous centre, but retains its separate identity for a brief period only.
19. Both the opercular process and the processus tympanicus petrosi caudalis chondrify in continuity with the otic capsule.
20. The processus tympanicus petrosi caudalis and the processus recessus develop relatively late in ontogeny.
21. The otic capsule ossifies from various centres but three main ossification centres could be distinguished.
22. The processus opercularis displays an autogenous ossification centre.
23. The prominentia utriculo-ampullaris anterior and the prominentia semicircularis lateralis are the last portions of the otic capsule to ossify.
24. The caudal petrosal tympanic plate ossifies in continuity with the otic capsule.

d. *Ala temporalis.*

1. The ala temporalis is nearly horizontally placed.
2. The foramen ovale is present.
3. The arteria infraorbitalis remains lateral and ventro-lateral to the ala temporalis and never pierces the latter structure.
4. The pterygoid process of the ala temporalis is already invaded by the pterygoid bone at an early stage of its development.
5. The ala temporalis is joined to the central stem and the cochlear capsule by the processus alaris and the alicochlear commissure respectively.
6. The ala temporalis chondrifies from a autogenous centre.

VOL
28
194

7. The alisphenoid ossifies from two centres—one in the pterygoid process and the other in the antero-lateral process of the ala temporalis.
8. The alisphenoid expands in dermal bone fashion.
9. The outer upper edge of the alisphenoid becomes fused with the pars entoglenoidea squamosi thus participating in the formation of the postero-ventral shelf of the glenoid fossa.

e. *Ala orbitalis.*

1. The apical portion of the ala orbitalis rests on the postero-lateral aspect of the cupula posterior of the nasal capsule.
2. The taeniae opticae are very slender and they are joined to the central stem by means of a slender common root.
3. The optic foramen is situated far laterally.
4. A small ala hypochiasmata is present.
5. The orbitoparietal commissure is deficient.
6. A short anterior clinoid process is present and it ossifies from a separate centre.
7. Both the ala orbitalis and the ala hypochiasmata arise from autogenous centres.
8. The ala orbitalis does not join the central stem until fairly late in ontogeny.
9. The orbitosphenoid ossifies from a centre in the medial aspect of the preoptic root.
10. In the juvenile animal the orbitosphenoid, which expands in dermal bone fashion, fuses with the mesethmoid in several places.
11. The foramen rotundum is confluent with the large foramen sphenorbitale (for. lacerum anterium).

f. *Nasal capsule.*

1. The lamina cribrosa is steeply inclined backwards thus being more pronounced precerebral than subcerebral.
2. The turbinal cartilages are nearly horizontally placed, being only very slightly inclined forwards and downwards.
3. No foramen epiphaniale is present.
4. An extensive incisura maxillo-atrioturbinalis separates the maxillo- and atrioturbinals.
5. A zona annularis is present.
6. The nasolacrimal duct runs forwards inside the zona annularis.
7. The fenestra superius nasi is well developed.
8. Both a processus alaris superior and a processus alaris inferior are present.
9. The processus alaris superior is attached to the antero-lateral corner of the processus lateralis ventralis by means of a slender root.

10. A processus cupularis (proc. alaris medius) is well defined.
11. The anterior paraseptal cartilage is strongly developed but an "outer bar" is present for a brief period in ontogeny only, being resorbed again soon after its formation.
12. The cartilago ductus nasopalatini is well developed but fused to the antero-ventral aspect of the anterior paraseptal cartilage.
13. A separate cartilago palatini is not present but the latter is probably represented by a short backwardly directed spur on the cartilago ductus nasopalatini.
14. No cartilago papillaris palatinae was found.
15. The posterior paraseptal cartilage has a strongly developed posterior spur but only a very short anterior spur which is invaded by the vomer at a very early stage of its development.
16. The nasal septum is the first part of the nasal capsule to chondrify.
17. The paries and tectum nasi chondrify from three pairs of centres.
18. The lamina cribrosa has no separate chondrification centre.
19. The growth of the zona annularis round the outside of the ductus naso-lacrimalis is a secondary development.
20. The anterior paraseptal cartilage arises from an autogenous chondrification centre.
21. No separate chondrification centre could be detected for the posterior paraseptal cartilage.
22. The cartilago ductus nasopalatini chondrifies in continuity with the anterior paraseptal cartilage.
23. In its post optimal development the anterior paraseptal cartilage becomes detached from the lamina transversalis anterior.
24. Similarly the proboscis acquires extreme movability due to extensive resorption of cartilage in the tectum, paries and septum nasi opposite the incisura maxillo-atrioturbinals.
25. The nasoturbinals ossify from separate centres.
26. The lateral pleurethmoids each ossifies from several centres, the main ossification centre being situated in the first primary ethmoturbinal.
27. A well defined mesethmoid ossification centre could be distinguished towards the centre of the joined cribriform plates.
28. This mesethmoid ossification centre appears in the juvenile Suncus some time after birth.
29. The maxilloturbinals ossify from autogenous centres and later on fuse with the maxilla.

g. *Supraoccipital cartilage.*

1. The supraoccipital cartilage is not exceptionally wide and it displays normal relations.

VOL.
28
194

2. It bears an inconspicuous antero-ventrally directed outgrowth (proc. opercularis, FAWCETT) which, however, is concluded to have nothing to do with the processus opercularis on the crista parotica.
3. Due to the lack of critical intermediate stages the earliest development of the supraoccipital cartilage and supraoccipital bone could not be determined.

h. *Dermal bones.*

1. The premaxilla has a well developed processus palatinus medialis (proc. prevomeralis) which, however, has no separate ontogenetic identity.
2. The palatine process of the premaxillae completely fuse with each other during the later stages of development.
3. The maxilla bears a short zygomatic process which does not ossify from an autogenous centre.
4. During the later stages of development the palatine processes of the maxillae become completely fused.
5. The infraorbital foramen is delimited postero-dorsally by the lacrimal bone which later on becomes fused with the maxilla.
6. The maxilla is pierced for a considerable distance by the nasolacrimal canal.
7. The jugal is entirely absent and the zygomatic arch most incomplete.
8. The laminae horizontales of the palatines fuse at a relatively early stage of development.
9. The palatine ossifies from a single centre situated near the junctional point of the horizontal and vertical laminae.
10. The vomer invades the posterior paraseptal cartilages and the laminae transversales posteriores at an early stage of development and later on becomes inseparably fused with the ethmoid.
11. The vomer ossifies from paired lateral centres.
12. A strongly developed pterygoid cartilage is present.
13. The pterygoid arises from a single centre.
14. The junction between the nasals and frontals is roughly chevronshaped with the apex directed backwards.
15. The two nasals are fused with each other.
16. The frontals fuse with the parietals during the later developmental stages and also with the ethmoid ossification.
17. The anterior end of the parietal, in the late developmental stages, becomes fused with the squamosal.
18. The squamosal displays a well defined processus postglenoideus and glenoid fossa but it bears no zygomatic process.
19. The squamosal ossifies from a single centre situated in the processus postglenoideus.

20. The tympanic (ectotympanic) bone retains its characteristic horsehoe shape throughout life.
21. The gonial (prearticular) displays normal relations and is pierced by a foramen for the transmission of the chorda tympani nerve.
22. The interparietal is extensive and soon after its formation it becomes inseparably fused with the supraoccipital.

PART II. ELEPHANTULUS MYURUS JAMESONI (CHUBB).

I. INTRODUCTION.

For a brief historical review of the Family *Macroscelidae* and its possible relations to the other "Insectivores" and Marsupials the reader is referred to the introductory chapter on *Suncus orangiae*. Here the views of BROOM (1902 and 1915), GREGORY (1910), ELLIOT SMITH (1902), PARKER (1886), CARLSSON (1909 and 1922), LE GROS CLARK (1928), SIMPSON (1931) and SONNTAG (1925) are discussed in short.

Elephantulus myurus jamesoni (Fam: Macroscelidae) dealt with in this paper, was first described by CHUBB (1909) as *Elephantulus rupestris jamesoni*. This was considered to be a supspecies of *E. rupestris*, described by SMITH (1830) as *Macroscelides rupestris*. The type locality was given by SMITH as the "mountains near the mouth of the Orange River". THOMAS and SCHWANN (1906) removed this species from the genus *Macroscelides* to a new genus *Elephantulus*. ROBERTS (1924) found that *E. rupestris* was specifically distinct from a previously believed subspecies *E. rupestris myurus* (THOMAS and SCHWANN). Furthermore he found that *E. rupestris jamesoni* (CHUBB) was actually a subspecies, not of *E. rupestris* as was thought before, but of the newly established *E. myurus*. Subsequently, therefore, *E. myurus myurus* (THOMAS and SCHWANN) *E. myurus jamesoni* (CHUBB) and *E. myurus mapogonensis* (ROBERTS) became three subspecies of the newly established *E. myurus*.

II. MATERIAL AND TECHNIQUE.

The embryonic material of *Elephantulus myurus jamesoni* was collected mainly at Bronkhorstspruit, Eastern Transvaal, and fixed in Bouin solution. After decalcification in Ebner's solution and neutralization the heads of the embryos were dehydrated and embedded in paraffin wax (m.p. ± 54° C).

Transverse serial sections were cut at a thickness of 10 μ in the younger and 15 μ in the older embryonic stages.

The material was first sectioned and then stained with Hansen's haematoxylin and Eosin. The crown-rump measurements of the embryos used were: 7.4 mm; 10.5 mm; 11 mm; 12 mm; 12.2 mm; 14 mm; 14.1 mm; 15.5 mm; 17 mm; 20 mm; 26 mm; 30 mm and 34 mm.

III. THE CHONDROCRANIUM.

As in the previous and in subsequent papers FAWCETT's (1917) descriptive method will chiefly be followed.

In the 17 mm Elephantulus embryo the chondrocranium is seen at about its optimal stage of development and this stage will therefore be described in more detail with subsequent reference to the younger and older stages. However, DU TOIT (1942) has described the nasal region of the Elephantulus chondrocranium in detail so this will be omitted in the present discussion.

A. THE CENTRAL STEM.

Morphologically the Mammalian central stem is composed of: (I) The basal plate—related to the anterior end of the notochord, (II) The lamina hypophyseos—prechordal in position and related to the canalis cranio-pharyngeus and interna carotid arteries and (III) The trabecuar plate—(Pars Interorbitonasalis of FAWCETT).

The *basal plate* in Elephantulus has the characteristic triangular shape found in most Mammals. Its base, forming the anterior margin of the foramen magnum, is wide and thin but its anterior portion is extremely narrow and thick. This part is triangular in cross-section, with the apex directed ventrally (figs. 29, 30). This marked constriction can probably be attributed to the pronounced medial extension of the cochlear capsules (fig. 27). The notochord can still be distinguished as a delicate median rod embedded in the anterior part of the basal plate (figs. 28, 29, 30). In the posterior half of the basal plate however, the notochord emerges on the upper or cerebral surface of the plate and in the basal portion, where perichondral ossification has already set in, it is completely resorbed. The extreme anterior tip of the notochord is strongly inclined dorsally and emerges on the upper surface of the basal plate below the posterior end of the hypophysis, thus becoming intracranial again.

Regarding its relations to surrounding structures the basal plate presents nothing of particular interest. A wide basicochlear fissure separates its anterior part from the cochlear capsule and a well defined basi-vestibular commissure (DE BEER 1937) or chordo-cochlear commissure (FAWCETT 1917) is present.

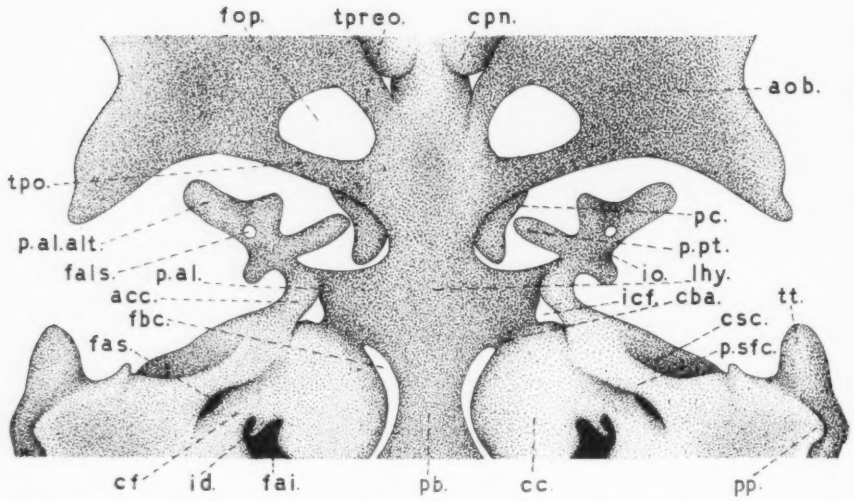

Fig. 27. Dorsal view reconstruction of the sphenoidal region of the chondrocranium of a 17 mm embryo (× 18).

A single pair of hypoglossal foramina indicate the line of fusion of the basal plate with the exoccipital cartilages.

The *lamina hypophyseos* (fig. 27) in Elephantulus has the form of a transversely placed rectangle about twice as wide as the anterior end of the basal plate with which it is fused. This is probably due to the exceptional degree of constriction of the anterior end of the basal plate by the two cochlear capsules. The connections of the lamina hypophyseos with the rest of the central stem, with the alae temporales, alicochlear commissures and cochlear capsules are typically Mammalian and do no differ in any important respect from the conditions described for Suncus. Unlike Suncus and Sorex (DE BEER) Elephantulus has a fairly well defined dorsum sellae and fossa hypophyseos.

The *trabecular plate* in Elephantulus is much wider in its posterior part than in Suncus and posterior to the optic foramina it is slightly concave above, but it rapidly becomes cylindrical between the orbito-nasal fissures and laterally compressed intranasally. The pre- and post optic roots of the ala orbitalis are thick and join the postero-lateral border of the trabecular plate separately (fig. 27).

The intranasal portion of the trabecular plate has been discussed in full by DU TOIT (1942).

1. Foramina in the Central Stem: At the optimal stage of chondrification both the fenestra hypophyseos (fenestra basicranialis anterior) and the fenestra basicranialis posterior are absent.

The carotid foramina are typically placed, although a bit far laterally on

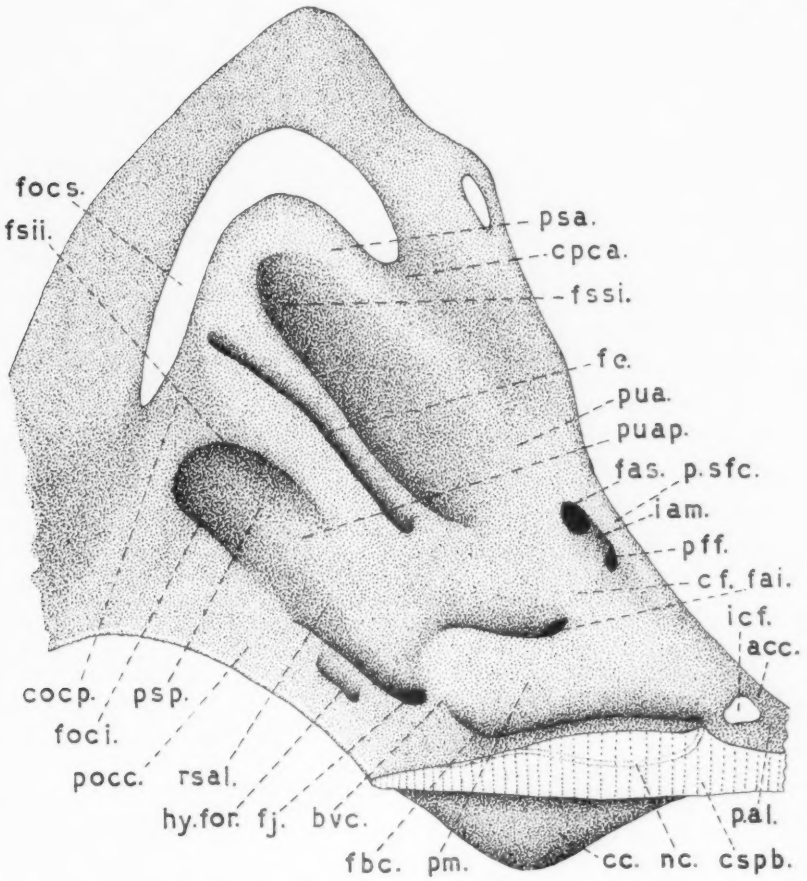

Fig. 28. Medial view reconstruction of the auditory capsule of a 17 mm embryo of *Elephantulus myurus jamesoni* (× 24).

account of the very wide lamina hypophyseos separating them. Each is bound laterally by a complete alicochlear commissure.

2. Early development of the central stem: In contrast to typical "Insectivores" the cephalic flexture in the Elephantulus central stem is pronounced, particularly so during the early embryonic stages. It may be mentioned here that an inconspicuous cephalic flexture seems to be characteristic of the typical "Insectivores". LEIMGRUBER (1939) mentions "a stretched central stem without bending" in Centetes and claims this to be an Insectivore feature. Suncus conforms to the condition described for Centetes but not so with Elephantulus.

The basal plate in Elephantulus shows no signs of either a fenestra basicranialis posterior or of paired parachordals at any stage of its development.

Similarly the fenestra hypophyseos is obliterated, even in blasteme, at a very early stage; being completely absent in the 10.5 mm embryo. Noteworthy, however, is the separation between the trabecular plate and the lamina hypophyseos which persists in the 10.5 mm embryo although at this stage the central stem is densely blastematous and even slightly chondrified in places (fig. 33).

No traces of paired polar elements could be detected in the early development of the lamina hypophyseos.

By contrast with Suncus the basicochlear fissure in Elephantulus appears early. It could be detected with ease in the earliest blasteme stages of the cranium investigated and does not disappear till ossification is far advanced.

Chondrification of the central stem commences and proceeds exactly as in Suncus. The first indications of chondrification were observed in the 10.5 mm embryo.

The relations of the Elephantulus notochord to the basal plate is different from Suncus. The position of the notochord in the 17 mm embryo of Elephantulus has already been described, and exactly the same relations are found in the earliest stages of development except that in these stages the notochord is still complete and not interrupted anterior to the odontoid process. In TOURNEUX's (1912) classification of notochord types (quoted after STADTMÜLLER 1936) the notochord of Elephantulus can be regarded as transitional between the retrobasilar and the basilar types. BOLK (1922) classifies the notochord differently and reports a condition similar to that found in Elephantulus in the sheep. He regards this condition as intermediate between his intrabasilar and transbasilar types.

3. Post optimal changes in the central stem: The Mammalian central stem is said to ossify, as a rule, from four centres. These are from before backwards: the mesethmoid, presphenoid, basisphenoid and basioccipital.

The *mesethmoid* will be discussed under the nasal capsule.

The *presphenoid* in Elephantulus arises from a pair of centres on the central stem medial to the large optic foramina. In the 26 mm embryo these centres are present and separated by a fairly wide strip of cartilage but soon afterwards they fuse completely over the midline of the central stem. The relations of the presphenoid to the orbitosphenoid are discussed with the orbitosphenoid.

The *basisphenoid* in Elephantulus arises from an unpaired median centre in the lamina hypophyseos.

In the 20 mm stage the first signs of perichondral ossification were observed in this region. During later levelopment the basisphenoid becomes indistinguishably fused with the alisphenoid as is usually the case. As far as I could make out from the embryonic material at my disposal the basisphenoid does not

VOL
28
194

bear any definite processus tympanicus basisphenoidei in Elephantulus, although it does roof the anterior medio-dorsal aspect of the rostral portion of the tympanic cavity.

The *basioccipital* in Elephantulus is essentially the same as in Suncus, except that its ossification centre in the basal plate arises a short distance anterior to the incisura intercondyloidea and not on its anterior margin. This centre could already be faintly distinguished in the 15.5 mm embryo.

B. LATERAL STRUCTURES APPENDED TO THE CENTRAL STEM.

The foramina lying between these lateral structures and the central stem will be discussed with the lateral structures concerned.

1. The exoccipital cartilage of Elephantulus agrees in general with that of Suncus and will not be discussed in detail.

The paracondyloid process giving attachment to the musculus rectus capitis lateralis and formed by the junction of the anterior margin of the lamina alaris with the pars canalicularis behind the jugular foramen is less conspicuous in Elephantulus than in Suncus. Also the recessus supra-alaris which lodges the terminal part of the lateral sinus is much narrower in Elephantulus.

Postero-dorsally the recessus supra-alaris is continued into the fissura occipito-capsularis inferior (posterior) (fig. 28). This fissure is separated from the fissura occipito-capsularis superior (fissura capsulo-parietalis or foramen jugulare spurium) by the posterior occipito-capsular commissure, which joins the cupula posterior of the pars canalicularis to the exoccipital.

Only a single pair of hypoglossal foramina is present at the level of the junctional zone between ex- and basioccipital cartilages.

a. *Early development of the exoccipital cartilages:* The exoccipital cartilages in Elephantulus definitely arise from autogenous chondrification centres as is typical for Mammals. In the 10.5 mm embryo the basal ends of the exoccipitals and the basal portion of the planum basale were found to be slightly chondrified, but these chondrification centres were clearly separated by dense mesenchyme. Even in the 12.2 mm embryo a narrow intervening strand of procartilage was found between the exoccipital cartilage and the basal plate. Compared to the rest of the occipital region the lamina alaris of the exoccipital develops relatively late in Elephantulus, being entirely procartilaginous in the 15 mm embryo. During later development the anterior edge of the lamina alaris becomes fused with the pars canalicularis of the otic capsule, but never does it display the same intimate connections as in Suncus. In the 12.2 mm embryo the connections of the exoccipital cartilages with supraoccipital and with the cupulae posteriores of the otic capsules (through the

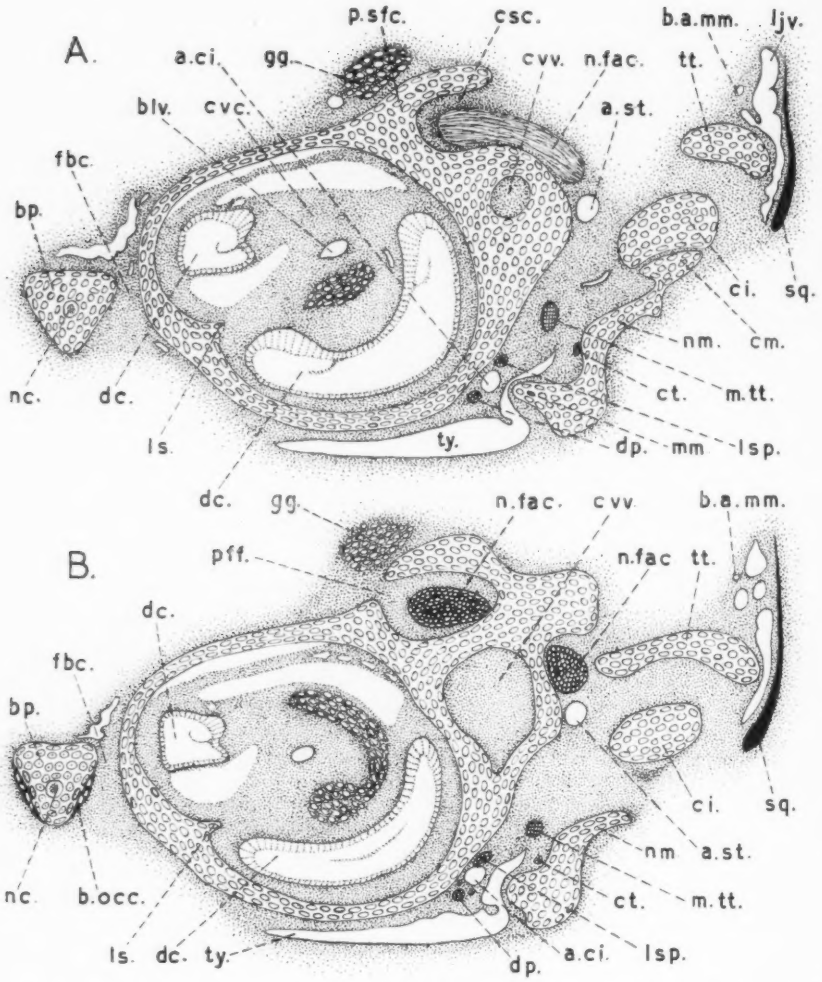

Fig. 29 A—B. Consecutive transverse sections through the front of the auditory capsule of a 17 mm embryo (× 30).

posterior occipitocapsular commissures) were found to be still entirely blastematous. In the 14.1 mm embryo cartilaginous continuity is established.

b. *Post optimal changes in the exoccipital cartilages:* In Elephantulus the ossification of the exoccipital cartilage proceeds in much the same way as in Suncus, except that the processus paracondyloideus does not ossify from a separate centre. The first signs of ossification in the exoccipital region were seen in the 17 mm embryo where it was already fairly extensive. Although merely perichondral, it involved the major part of the exoccipital cartilage.

2. The auditory capsule of Elephantulus (figs. 27, 28) conforms

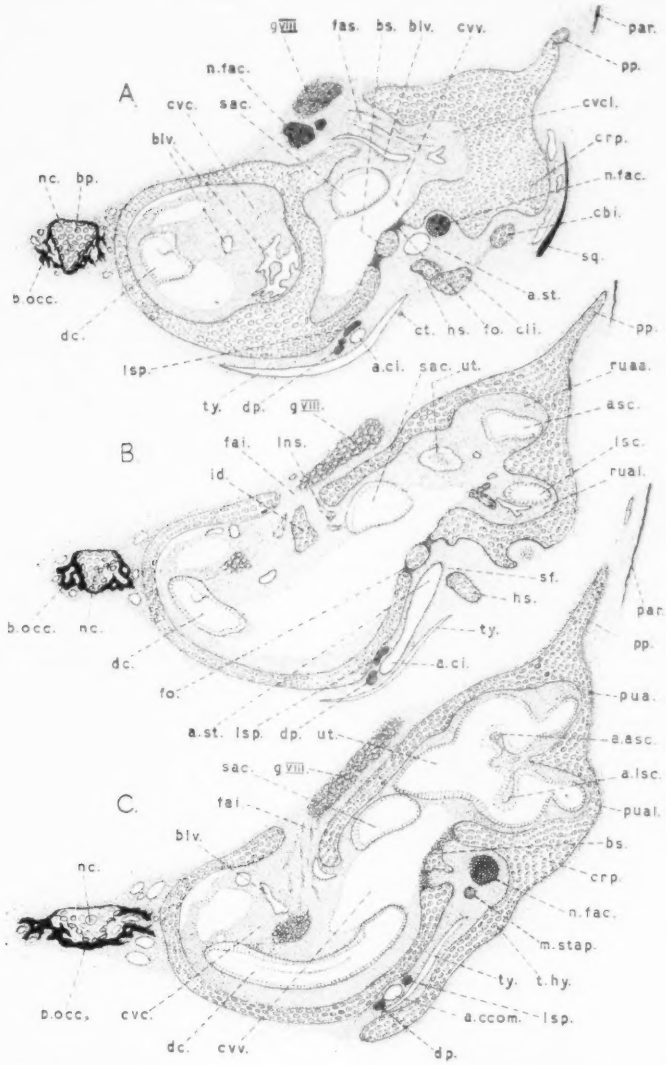

Fig. 30 A—C. Consecutive transverse sections through the auditory capsule of a 17 mm embryo (× 20).

to the general Mammalian plan and a detailed regional description will therefore not be given.

In general form, the auditory capsule is more markedly quadrilateral than in Suncus, the long axis passing obliquely upwards and backwards. Further, the pars canalicularis in Elephantulus is more highly elevated above the plane of the basal plate (fig. 28) while conversely the portion of the pars cochlearis projecting below the plane of the basal plate is much larger than in Suncus.

The pars cochlearis, especially its cochlear segment, is smaller, but the antero-ventral convergence of the two cochlear capsules is far more pronounced in Elephantulus, thus constricting the anterior part of the planum basale to a much larger extent (fig. 27).

With regard to the attachments of the auditory capsule we find that because the fissura basicochlearis is undivided the so-called anterior chordo-cochlear commissure of Suncus is absent in Elephantulus. The presence of a narrow fissura occipito-capsularis inferior (posterior) results in the isolation of a commissura occipito-capsularis posterior which joins the cupula posterior of the pars canalicularis to the exoccipital.

The lamina parietalis is inconspicuous. It has no anteriorly directed process but it is wide and springs from the anterior dorsolateral edge of the pars canalicularis. It has a wide base and projects upwards and backwards to join the supraoccipital (fig. 28). The fissura occipito-capsularis superior is very wide but there is no anterior prolongation of the supraoccipital (so-called processus opercularis of FAWCETT 1917) which overlaps this fissure.

VOL
28
194

The tegmen tympani is massive. It has the form of a wide horizontal plate slightly concave below and fused postero-medially with the pars canalicularis (figs. 27, 29). Posteriorly and postero-laterally the tegmen tympani is continued into the crista parotica.

A real processus opercularis is entirely absent in Elephantulus. The lateral jugular vein which in Suncus runs forwards and downwards from the foramen jugulare spurium over the base of the commissura parieto-capsularis anterior and which is lodged in a deep sulcus and protected by the processus opercularis does not occupy this position in Elephantulus. In Elephantulus it runs forwards medial to the base of the commissura parieto-capsularis anterior and consequently both the deep sulcus and the opercular process are missing.

Compared to Suncus the crista parotica of Elephantulus is far more massive and posterior to the root of the tympano-hyale it is continued for some distance backwards as a prominent roof over the anterior part of the sulcus musculi stapedii (fig. 31).

On its medial surface the pars canalicularis is deeply indented by the fossa subarcuata superior interna which is long and ovoid, and whose longitudinal axis coincides with the longitudinal axis of the auditory capsule (fig. 28).

The essential relations of the suprafacial commissure are similar in Suncus and Elephantulus but it is a much thicker and stronger rod in Elephantulus. The cavum supracochleare in Elephantulus is not bordered by a bridge over the foramen faciale externum vel secundarium since this foramen does not exist in the chondrocranium of Elephantulus [cf. Microtus (FAWCETT 1917)]. The facial nerve runs from the cavum supracochleare round the anterior border of the vestibular segment and enters the sulcus facialis.

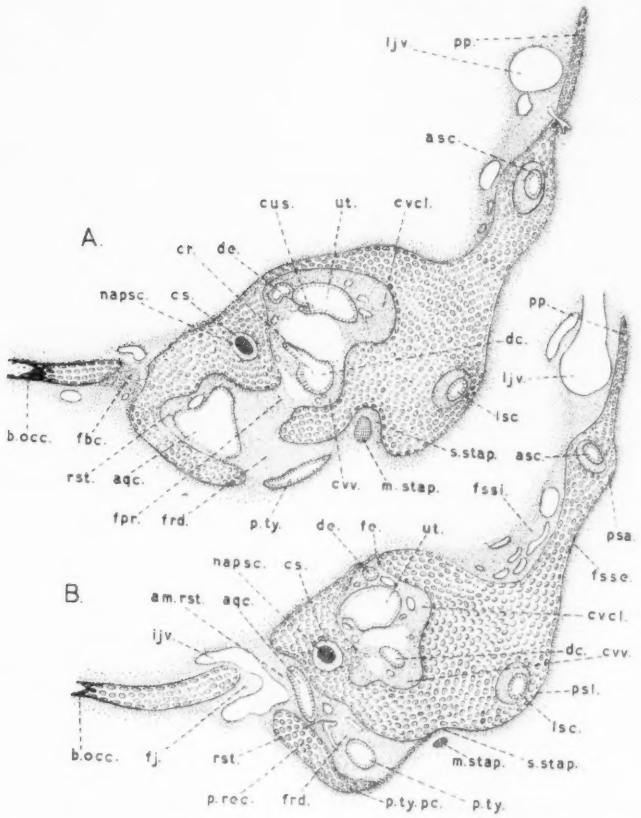

Fig. 31 A—B. Consecutive transverse sections through the pars canalicularis of the auditory capsule of a 17 mm embryo (× 20).

The infero-medial surface of the pars canalicularis is remarkable because it displays a large fossa subarcuata inferior (posterior) interna which is clearly separated anteriorly from the recessus supraalaris by the prominence of the recessus utriculo-ampullaris posterior and the posterior semicircular canal (fig. 28). Posteriorly this prominence disappears and the fossa subarcuata inferior interna merges with the recessus supra-alaris, and together they lead into the fissura occipito-capsularis inferior. Laterally the pars canalicularis shows a shallow fossa subarcuata superior externa which is pierced at its base by several small bloodvessels (fig. 32).

Externally the pars cochlearis shows no peculiarities except that a sulcus septalis and a sulcus for the stapedial artery are absent. These may, however, appear during later development.

a. *Foramina in the walls of the auditory capsule:* In the medial wall of the vestibular segment the meatus auditorius internus leads into the primary

facial foramen anteriorly while posteriorly it leads into the foramen acusticum superius and inferius. In the latter foramen a small spur of cartilage is attached to the antero-medial aspect of the crista falciformis which partly isolates a foramen for the transmission of the lower nerve to the saccule (fig. 27). At a later stage (20 mm embryo) the posterior end of this spur becomes continuous with the medial edge of the crista falciformis thus forming a complete foramen for the lower saccular nerve as in Suncus and Microtus. The greater part of the foramen acusticum inferius transmits the cochlear nerve. Through its extreme posterior tip, however, the nerve to the ampulla of the posterior semicircular canal enters the foramen, or rather it enters the canalis singulare. This canal leads backwards through a massive ridge on the ventral surface of the medial wall of the cochlear capsule (fig. 31). This ridge, which partly separates the vestibular segment of the pars cochlearis from the cochlear segment, is more massive in Elephantulus than in Suncus. Anteriorly it arises from the ventrally deflected border of the crista falciformis and the posterior border of the crista falciformis and the posterior border of the foramen acusticum inferior; posteriorly it is continued into the medial edge of the floor of the pars canalicularis. The canalis singulare leads backwards into the floor of the posterior part of the pars canalicularis and opens on the dorsal aspect of the floor directly in front of the posterior semicircular canal. The foramen endolymphaticum is a long narrow fissure in the medial walls of the prominentia uticulo-ampullaris posterior and the prominentia cruris communis. Emerging from the cavum canaliculare relatively far forward the ductus endolymphaticus runs backwards in the long foramen endolymphaticum but it does not re-enter the auditory capsule as in Suncus. The commissura basicochlearis posterior is extremely narrow in Elephantulus and connects the medial wall of the posterior tip of the pars cochlearis, which contains the recessus scalae tympani, to the lateral edge of the basal plate. Behind the commissura basicochlearis posterior the medial wall of the recessus scalae tympani is deficient forming the apertura medialis through which the perilymphatic duct enters the cranial cavity. At the level of the anterior border the apertura medialis, however, the processus recessus also loses contact with the lateral border of the basal plate, thus forming the jugular foramen. The medial openings of the recessus scalae tympani and the jugular foramen are therefore confluent (fig. 31 b). In Elephantulus the constituent parts of the fissura metotica (viz. the apertura medialis and the jugular foramen) are not separate. This denotes the primitive condition. Posterior to the apertura medialis of the recessus scalae tympani the processus recessus merges into the floor of the prominentia utriculo-ampullaris posterior lateral to the posterior margin of the jugular foramen.

The fenestra rotunda is situated in the ventro-lateral wall of the recessus scalae tympani (fig. 31). A cartilaginous shelf lies below the posterior

VOL 28 194

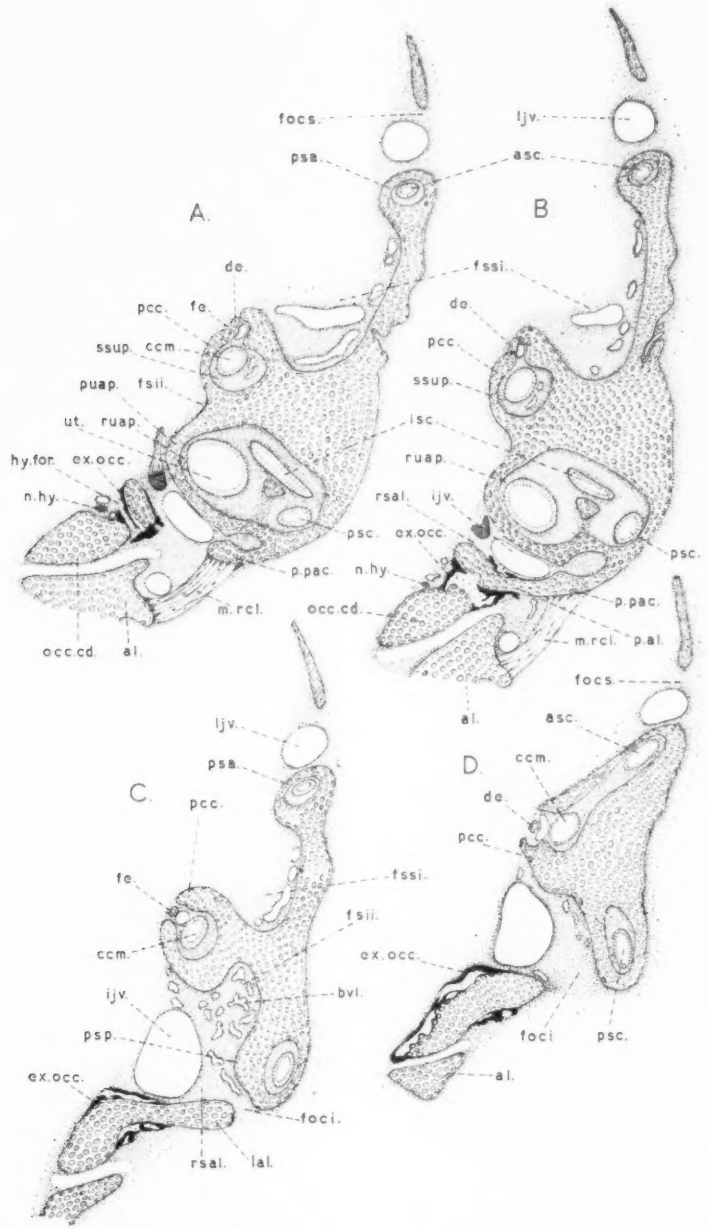

Fig. 32 A—D. Consecutive transverse sections through the pars canalicularis of the auditory capsule of a 17 mm embryo (× 20).

extremity of the middle ear. The medial wall of this shelf is fused to the lateral edge of the processus recessus so that posteriorly the fenestra rotunda lies at the base of a deep sulcus. This cartilaginous shelf undoubtedly represents a rudimentary caudal petrosal tympanic plate.

The fenestra ovale (vel vestibuli) (fig. 30) is related in the usual way to neighbouring structures.

b. *Early development of the auditory capsule:* The early development of the auditory capsule in Elephantulus does not differ in any important respect from that of Suncus, but it confirms the relatively late appearance of the processus recessus and the cartilaginous preformation of the caudal tympanic plate (processus tympanicus petrosi caudalis) which develops in continuity with the auditory capsule.

Two primary chondrification centres—one in the pars canalicularis and the other in the pars cochlearis could be distinguished.

c. *Post optimal changes in the auditory capsule:* The auditory capsule in Elephantulus was found to ossify as in Suncus except for the absence of a separate ossification centre in the extreme anteroventral aspect of the pars cochlearis. Furthermore a separate ossification centre could be distinguished in the tympano-hyale. This centre, however, does not retain its separate identity for long before becoming fused with the rest of the auditory capsule.

The caudal petrosal plate ossifies very late. It is still almost entirely cartilaginous in the 34 mm embryo. This can probably be explained by the very late associated ossification of the posterior canalicular portion of the auditory capsule. The caudal petrosal plate in Elephantulus greatly increases in size during later development, but unfortunately the lack of late prenatal and early postnatal stages made it impossible to trace the ultimate fate of this interesting element. One can, however, surmise that it plays an important part in the formation of the posterior extremity of the adult osseous bulla.

A small rostral entotympanic was found in Elephantulus. In the 30 mm embryo it was observed initially as a small piece of cartilage entirely separate from the cartilago tubae auditivae and lying medial to the rostral portion of the tympanic cavity between the ectotympanic and the basisphenoid. Later on it becomes totally fused with the horizontal caudal plate of the cartilago tubae auditivae. This development of the rostral entotympanic corresponds to that described by VAN DER KLAAUW (1929 and 1922) in certain other Mammals.

The absence of a separate caudal entotympanic in Elephantulus is remarkable since this element appears to be a very constant feature in the Macroscelidae. The oldest stage investigated was a 34 mm embryo, so that a caudal entotympanic may yet develop. But this is unlikely since the caudal entotympanic usually makes its appearance before the rostral entotympanic which is already present in the 30 mm embryo. VAN KAMPEN (1904, 1905) would not have supposed the caudal entotympanic of Elephantulus to develop later since he believed

VOL 28 194

the entotympanic (caudal entotympanic of VAN DER KLAAUW) and the caudal petrosal plate to be homologous. As VAN DER KLAAUW (1929) pointed out, VAN KAMPEN's view was held because he knew of no animal in which both an entotympanic and a real processus tympanicus petrosi caudalis occurred together. VAN DER KLAAUW (1922) has since described both entotympanics as well as a caudal petrosal plate in Rousettus and in 1929 he reported both entotympanic elements and a caudal petrosal plate in a number of Macroscelidae, so that VAN KAMPEN's assumption of the absolute homology was probably erroneous. On the other hand VAN DER KLAAUW observed a fusion of the caudal entotympanic with the petrosal plate in Rousettus and stated: "The possibility of the simultaneous presence of an entotympanic and a processus tympanicus petrosi warns us to be prudent in comparing every petrosal plate with an entotympanic. Of course it remains possible that the entotympanic secondarily loses its independence and fuses with the periotic very early in ontogeny, and even shows "fusio primordiale", but this is no longer the only possibility. It is also possible that a processus tympanicus petrosi is a real plate of the petrosal which has nothing to do with an entotympanic" (VAN DER KLAAUW 1929, p. 556). If one compares a section through the caudal petrosal plate of a 34 mm embryo of Elephantulus with a section through the same region of the Rousettus skull (VAN DER KLAAUW 1922, plate II, fig. 10) then the similarity of this plate in Elephantulus with the structure labelled "caudal entotymanic" in Rousettus is so striking that one has to admit the probability of a "fusio primordiale" in Elephantulus in which case the caudal petrosal plate in Elephantulus would have a double origin. KEEN and GROBBELAAR (1941), in a paper on the comparative anatomy of the tympanic bulla and auditory ossicles, mention the following elements as forming the bulla in the Macroscelidae: tympanicum, mastoid part of the periotic, alisphenoid, basisphenoid and squamosal. They do not mention the entotympanic elements at all. But since their investigation was carried out on dried adult skulls it is quite possible that these elements were fused with neighbouring skeletal elements and escaped their notice.

3. The ala temporalis (fig. 27) in Elephantulus is a relatively inconspicuous structure. Its attachments to the central stem and cochlear capsule correspond exactly with those of Suncus. The antero-lateral process of the ala temporalis is not, however, pierced by a fenestra ovalis. On its lateral side it merely shows a shallow notch, the incisura ovalis, for the mandibular nerve. This incisura is therefore homologous with the fenestra ovalis of other forms. The antero-lateral process in Elephantulus is slightly bifurcated anteriorly and on its dorsal surface it bears a deep groove for the arteria infraorbitalis. This groove ends posteriorly in the foramen alisphenoidale through which the artery enters the cranial cavity. A somewhat similar condition has been described by WATSON (1916) and DE BEER and FELL (1936)

for Ornithorhynchus and by ARNOLD (1928) for the ox. DE BEER (1936) maintains that the position of this foramen alisphenoidale in Ornithorhynchus represents the line of fusion between the processus alaris and the alisphenoid. Ontogenetic evidence in Elephantulus, however, does not support this statement.

The pterygoid process of the ala temporalis in Elephantulus is long and reaches forward and medialward and almost touches the lateral border of the pterygoid cartilage. A posterior spur of the pterygoid bone lies directly medial to the pterygoid process but does not invade this process.

The general position of the ala temporalis in Elephantulus is neither completely horizontal as in Suncus, nor is it vertical; but its outer border has a slight dorsal inclination.

a. *Early development of the ala temporalis:* In Elephantulus, as in Suncus, the ala temporalis shows an autogenous chondrification centre which makes its first appearance in the 12.2 mm stage. Shortly afterwards this cartilage joins the processus alaris of the lamina hypophyseos. The relations of the processus pterygoideus of the ala temporalis are exceptional and their significance is obscure. This process in Elephantulus was found to make its first appearance as a blasteme rudiment relatively late in ontogeny. It was found to be absent in the 10.5 mm embryo. On the other hand the 12.2 mm embryo showed a well developed blastematous processus pterygoideus which was closely applied to the postero-lateral aspect of the blastematous pterygoid cartilage. Blastematous continuity with the rest of the ala temporalis, however, was found to be extremely slight. Shortly after this stage the pterygoid process of the ala temporalis chondrifies from an autogenous centre but, although extensively chondrified, it does not join the rest of the ala temporalis till after the 14.1 mm stage.

b. *Post optimal changes in the ala temporalis:* The alisphenoid in Elephantulus ossifies from a single centre in the ala temporalis lateral to the foramen alisphenoidale. This centre was first observed in the 20 mm embryo where the lateral edge of the antero-lateral process of the ala temporalis was found to be well expanded in dermal bone fashion. The pterygoid process in Elephantulus does not ossify separately. Because of its invasion by the posterior end of the pterygoid in the late ontogenetic development the ala temporalis and consequently the alisphenoid becomes intimately fused with the pterygoid in this region. A processus tympanicus alisphenoidei is present in the older embryonic stages of Elephantulus. Since the specimens investigated were relatively young, however, this process of the alisphenoid was found not to be very well defined. It merely forms a roof to the rostral portion of the tympanic cavity. Where this roof is fused to the ventral aspect of the alisphenoid proper its lateral edge forms a slight crest on the ventral surface of the bone thus forming a crista lateralis bullae alisphenoidei which projects

VOL.
28
194

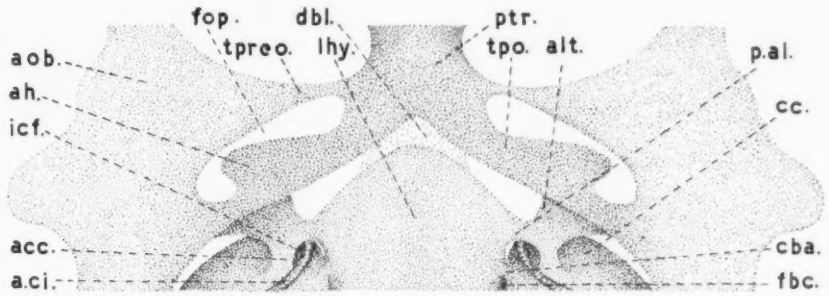

Fig. 33. Ventral view reconstruction of the blastem primordium of the sphenoidal region of the chondrocranium of a 10.5 mm embryo (× 45).

backwards for a short distance. The lateral surface of this crest participates in the formation of the ventral border of the glenoid cavity.

4. The ala orbitalis (fig. 27) in Elephantulus is massive. It is a wide cartilaginous plate which protects the brain antero-laterally and is markedly concave on its intracranial aspect. The anterior basal angle of the ala orbitalis is connected to the nasal capsule by the commissura sphenethmoidalis, but, as in Suncus, the orbito-parietal commissure is incomplete. The upper edge of the ala orbitalis in Elephantulus is partially invaded by the inner aspect of the frontal bone which partly overlaps the ala orbitalis dorso-laterally. Compared to Suncus the primordial optic foramina in Elephantulus are larger and are placed further medially. The extensive pre- and optic roots of the ala orbitalis join the trabecular plate separately. Although the preoptic root does not abut on the cupula posterior of the nasal capsule, as is often the case, it is closely related to it in its backward and medialward passage.

In the 17 mm embryo of Elephantulus dealt with at present, there is no structure comparable with the ala hypochiasmata of the other forms. The ala hypochiasmata was also reported as absent in Sorex and Talpa.

The orbitonasal fissure accupies the usual position and shows normal relations in Elephantulus.

a. *Early development of the ala orbitalis:* In Elephantulus, as in most Mammals, the ala orbitalis arises from a separate chondrification centre which is clearly distinguishable in the 11 mm embryo. Unlike Suncus, however, it fuses with the trabecular plate at a relatively early stage of its development. In the 12.2 mm embryo the ala orbitalis is completely fused both with the trabecular plate through its pre- and postoptic roots and with the nasal capsule through the commissura sphenethmoidalis. This is not surprising if one bears in mind that in the procartilaginous and blastematous stages the relations between the ala orbitalis and the central stem, in Elephantulus, are very intimate. Another peculiar feature of Elephantulus is that the ala hypochiasmata, although absent at the optimal stage of chondrification, is well

defined in the blastematous and early cartilaginous stages of the development of the ala orbitalis. Here it is confluent with the antero-medial border of the postoptic root (fig. 33) and serves as an attachment for some of the eye muscles. I was unable to decide whether or not it arises in earliest development from a separate centre as in Suncus. In later development it completely loses its identity. Its absence in Sorex and Talpa may possibly be explained in a similar way.

b. *Post optimal changes in the ala orbitalis:* The orbitosphenoid in Elephantulus ossifies from a single centre situated in the ala orbitalis anterolateral to the large optic foramen. Unlike Suncus, it was found that the presphenoid in Elephantulus ossifies from two centres distinct from the orbitosphenoids. These centres were found on either side of the presphenoidal region of the central stem just medial to the optic foramina. In the 26 mm embryo the two presphenoid centres, which are still separate from each other at this stage, were found to be fused with the orbitosphenoids through the slender taeniae preopticae. In the 20 mm stage bony continuity between the pre- and orbitiphenoids is established also behind the optic foramen through the taenia postoptica. The orbitosphenoid in Elephantulus, as in Suncus, forms a cup-shaped covering for the cupula posterior of the nasal capsule, but since the nasal capsule was still cartilaginous in the latest available stage the possibility of subsequent fusion of the orbitosphenoid and the ethmoid could not be determined.

5. The nasal capsule of Elephantulus at its optimal stage of chondrification has been described in detail by DU TOIT (1942) who also mentions some interesting facts about the postoptimal changes. In this paper, therefore, the author will only deal with the early development and some of the postoptimal changes.

a. *Early development of the nasal capsule:* In Elephantulus the early development of the nasal capsule conforms essentially to the development described for Suncus. In the 10 mm embryo the entire nasal capsule was found to be still blastematous. At this stage the tectum and paries nasi, although separate from the septum, merely show a pair of separate parietotectal centres; the more posterior paranasal and antorbital centres (TERRY) are already fused with each other. In the 11 mm embryo conditions were found to be not much different although all the centres participating in the formation of the nasal capsule are more or less fused. In the 12.2 mm embryo the greater part of the nasal capsule consists of young cartilage exclusive, however, of the pars anterior, the turbinals and the paraseptals which are still procartilaginous. It was therefore not possible to determine the exact course of the early chondrification in the nasal capsule but the stronger development of the posterior division of the nasal septum at this stage suggests that this was the first part of the nasal capsule to chondrify, as is usually the case.

VOL.
28
194

As in Suncus, the posterior paraseptal cartilage in Elephantulus, already present in the 14 mm stage, does not seem to arise from a separate chondrification centre, but appears to chondrify in continuity with the lamina transversalis posterior. That this condition is probably primary is also borne out by the fact that when the posterior paraseptal first makes its appearance in blasteme it is already in continuity with the blastematous lamina transversalis posterior.

The anterior paraseptal cartilage in Elephantulus is peculiar in that its blasteme rudiment in the 10 mm embryo is closely related to the blastematous nasal septum. As a matter of fact only an imaginary demarcation exists between the posterior and central divisions of the anterior paraseptal and the nasal septum at this stage. During the later stages of development, however, the anterior paraseptal definitely chondrifies from an autogenous centre. In both the 14 mm and 14.1 mm stages the greater central portion of the anterior paraseptal was found to consist of young cartilage while its anterior connection with the lamina transversalis anterior is still procartilaginous.

OL.
28
947

At no stage of its development is the anterior paraseptal cartilage (fig. 36) in Elephantulus in direct cartilaginous continuity with the nasal septum. The question arises whether the intimate blastematous relations between the anterior paraseptal and the nasal septum should be regarded as representing a primitive feature or merely as representing a phylogenetically insignificant secondary development. As these intimate relations are only displayed in the very early ontogenetic development where hardly any functional significance could be attributed to them, and as during the later stages of development these intimate relations become completely obscured one no longer feels inclined to doubt their primitive character. It will be recalled that LEVY (1909) reported a fusion of the anterior paraseptal with the nasal septum in Didelphys while OLMSTEAD (1911) maintained that in Canis familiaris the anterior paraseptal develops in continuity with the nasal septum. If these relations are primitive, as they are believed to be, they furnish additional proof for the old theory that the anterior paraseptal has to be regarded as a primitive element of the solum nasi which became secondarily associated with Jacobson's organ in Mammals.

b. *Post optimal changes in the nasal capsule:* In the oldest embryonic stage of Elephantulus at my disposal (34 mm) no indication was found of a separate mesethmoid ossification. It is possible, however, that the latter bone may still develop at a later stage as in the 34 mm embryo the presphenoid does not extend into the intranasal portion of the central stem.

C. THE DORSAL STRUCTURES.

The tectum posterius in Elephantulus, though more extensive than in Suncus, displays essentially similar relations to neighbouring structures. LEIM-

GRUBER (1939) reported a broad supraoccipital cartilage for Centetres, including this feature under the general characteristics of the Insectivores. As previously described, the supraoccipital cartilage in Elephantulus is fused with the exoccipital. At the junctional region between these two structures the posterior occipito-capsular commissure joins the occipital cartilages to the otic capsule thus isolating a superior occipito-capsular fissure. The supraoccipital bears no structure capable of identification with the so-called "opercular process" of FAWCETT.

1. Early development of the tectum posterius: The 12.2 mm embryo of Elephantulus displays the tectum posterius as an extensive blastematous plate in weak continuity both with the exoccipital and the parietal plate primordiae. At this stage the blastematous plate representing the "Anlage" of the two supraoccipitals is strongly procartilaginous along its posteromedial edge. Young cartilage could already be distinguished in the mid-dorsal line at the point of junction of the future supraoccipitals so that, as far as Elephantulus is concerned, the supraoccipitals definitely do not seem to chondrify from separate centres. On the contrary, they seem to arise from a single chondrification centre in the mid-dorsal line.

2. Post optimal changes in the tectum posterius: The first traces of ossification in the tectum posterius were observed in the 20 mm embryo of Elephantulus. At this stage the supraoccipital ossifications are fairly extensive but a narrow strip of cartilage was found still to intervene between the two ossification centres. Fusion of the supraoccipitals with the interparietal, which is non-existent at this stage, takes place later on.

VOL
28
194

IV. THE MEMBRANE BONES.

For a description of the membrane bones a 17 mm embryo of Elephantulus has been selected.

A. THE PREMAXILLA

of Elephantulus is essentially the same as that of Suncus. The processus palatinus medialis and the processus extranasalis are well developed and display more or less the same relations to neighbouring structures as in Suncus. The palatine processes of the premaxillae never fuse with each other at any stage of their development. The premaxillae also retain their separate identity throughout life, and in the adult Elephantulus the posteriorly directed spur of the processus extranasalis of the premaxilla is an extremely slender bony spur which extends backwards about half the total length of the nasal.

The first ossification in the premaxilla was encountered in the 13.5 mm embryo as a minute splint of bone in its future palatine process. From this centre the ossification was found to spread into the various parts of the premaxilla including the processus palatinus medialis.

B. THE MAXILLA.

The palatine process of the maxilla is not well developed in the 17 mm embryo of Elephantulus. The palatine processes of the two maxillae do not meet each other in the middle line at this stage and neither do they bear any close relations either with the vomer or with the processus palatinae mediales of the premaxillae. The infraorbital foramen pierces the maxilla so that the lacrimal bone does not take part in its formation as is the case in Suncus.

The zygomatic process of the maxilla is well developed and it joins the jugal. During the later stages of its development the maxilla in Elephantulus acquires the usual Mammalian relations to its adjoining skeletal elements. The palatine processes of the two maxillae, although intimately connected, retain a faint suture throughout life. Peculiar of the adult Elephantulus skull are the two sets of huge elongated fenestrae in the maxillary division of the secondary palate. These fenestrae, together with similar fenestrae in the palatal division of the palatines, and the large foramina incicivae render the false palate most incomplete.

The first indication af a maxillary ossification in Elephantulus was found in the 12 mm embryo in the future alveolar portion of the bone. During the early development of the maxilla a small but well defined nodule of secondary cartilage appears in the frontal process immediately postero-dorsal to the infraorbital foramen. This nodule of secondary cartilage indicates the origin of some facial muscles from the maxilla.

C. THE LACRIMAL BONE

in the 17 mm embryo of Elephantulus bears a conspicuous postero-laterally directed spur which lies on top of the zygomatic process of the maxilla. This spur of the lacrimal does not reach the jugal at this stage. It forms the dorsal antero-medial delimitation of the orbit, and the lacrimal canal pierces the lacrimal bone postero-medial to the attachment of this spur. Later in development of Elephantulus this postero-laterally directed spur of the lacrimal joins the extreme antero-dorsal tip of the jugal but it does not fuse with the adjacent bones at any stage of its development.

The lacrimal bone appears very late. The first trace of ossification in this region was observed in the 17 mm embryo of Elephantulus where it was found

to be already fairly extensive. In the 15.3 mm embryo, however, the lacrimal is still absent and its future position is indicated merely by a concentration of mesenchyme cells.

D. THE JUGAL.

In Elephantulus the zygomatic arch is complete and a well developed jugal participates in its formation as is the case in all the Menotyphla. There is, however, no indication of a postorbital bar in Elephantulus, not even of a processus postorbitalis on the frontal. In the 17 mm embryo the jugal is pierced by a number of small foramina for the transmission of small bloodvessels, but an extensive foramen malare could not be distinguished. At this stage the anterior end of the jugal articulates with the zygomatic process of the maxilla over a long distance but it does not reach quite as far forward as to establish relations with the lacrimal bone. Posteriorly the jugal joins the zygomatic process of the squamosal but it does not reach as far back as the glenoid cavity.

Except for the fact that the jugal later on gains continuity with the lacrimal bone no important changes take place during its later development. The ossification of the jugal in Elephantulus was first observed in the 14 mm embryo as a minute splint of bone lying in close proximity to the posterior extremity of the zygomatic process of the maxilla.

E. THE PALATINE.

In the 17 mm embryo of Elephantulus the laminae horizontales of the palatines are still widely separated, each being pierced by two foramina for the transmission of the medial palatine nerves. The lamina horizontalis forms the floor of the ductus nasopharyngeus of its corresponding side (fig. 34), this duct being paired anteriorly and single posteriorly. The vertical lamella of the palatine is pierced by a foramen for the transmission of a vein, and the dorsal edge of this lamella has the shape of a shallow trough lying under the lamina transversalis posterior as in Suncus. Behind the cupula posterior of the nasal capsule the vertical lamella is continued as a horizontal plate which extends as far back as the anterior end of the pterygoid. At this stage of development the palatine bears no close relations with the vomer. During the later stages of its development the horizontal laminae of the palatines meet in the mid-line, and, as has been mentioned before, they display three sets of large fenestrae. The antero-medial set of fenestrae is competely or partly confluent with the posterior set of fenestrae in the maxillary palatine process. Further back there are two more sets of fenestrae in the horizontal laminae of the palatines; these, a postero-medial and a lateral set, are completely isolated. As a matter of fact only a few delicate osseous bars, separating these extensive fenestrae,

VOL
28
194

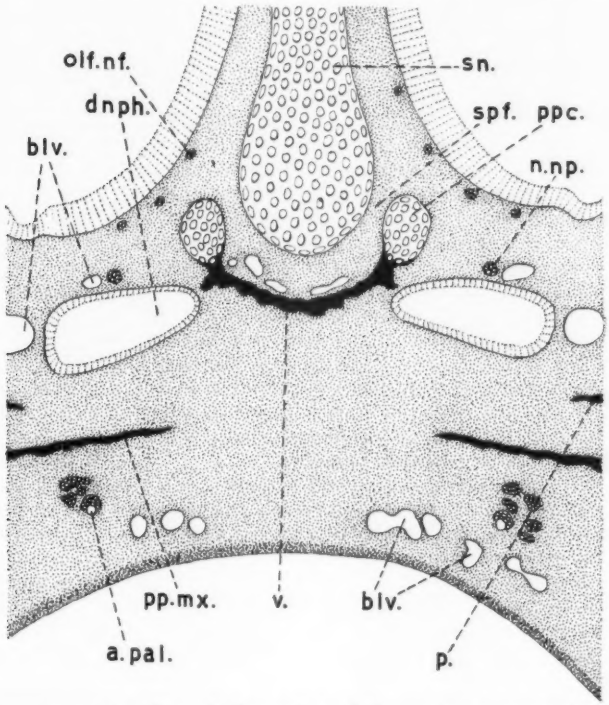

Fig. 34. Transverse section through the region of the posterior paraseptal cartilages and vomer of a 17 mm embryo (× 70).

constitute the laminae horizontales in the adult Elephantulus. STADTMÜLLER (1936) mentions that a fenestration of the horizontal laminae of the palatines is characteristic of the Marsupials and some Insectivores. The lamina verticalis of the palatine displays a large processus orbitalis in the adult Elephantulus.

The ossification of the palatine eminates from a single centre located at about the junctional point of the horizontal and vertical laminae. It was first observed in the 13.5 mm embryo.

F. THE VOMER.

In the 17 mm embryo of Elephantulus the vomer extends backwards from between the anterior paraseptal cartilages to a point medial to the roots of the posteriorly directed spurs of the posterior paraseptal cartilages. At this early stage of its development the vomer bears no close relations to any other bones in its vicinity and it has the shape of a plain shallow trough the dorsal edges of the posterior third of which invade the anteriorly directed spurs of the posterior paraseptal cartilages (fig. 34). Later in its development the vomer becomes inseparably fused with the ethmoid as in Suncus and it acquires the

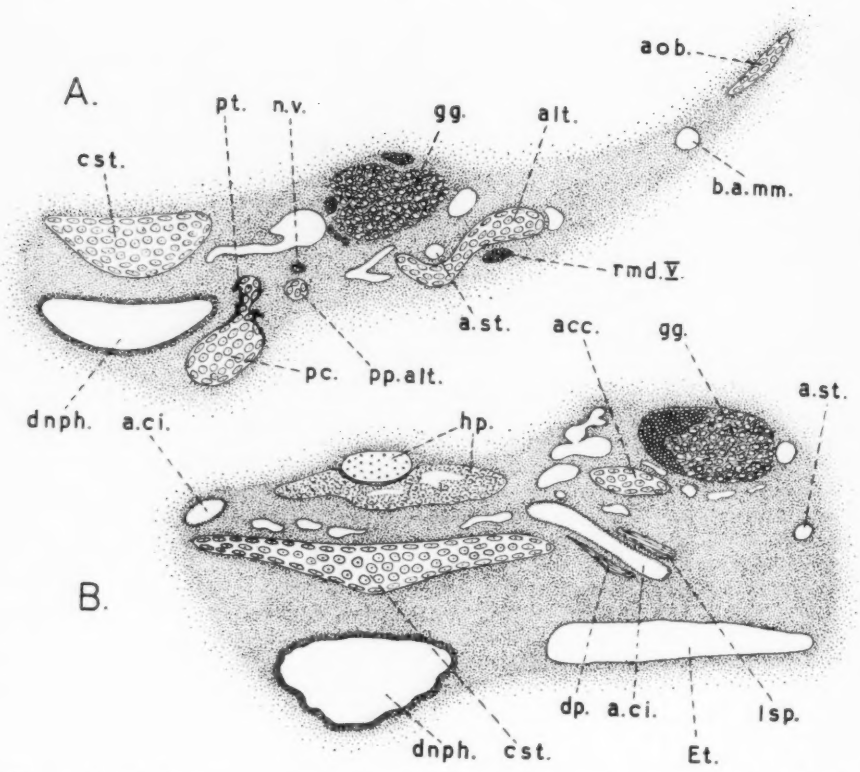

Fig. 35 A—B. Consecutive transverse sections through the posterior sphenoidal region of the chondrocranium of a 17 mm embryo (× 30).

usual relations to the adjacent elements. DU TOIT (1942) also mentions an invasion of the posterior paraseptal cartilage by the vomer in the 30 mm stage of Elephantulus. I was able to confirm beyond doubt the separate origin of the two lateral halves of the vomer in Elephantulus. In the 15.5 mm embryo the two halves were found to be still completely separate and each consists of two small splints of bone lying ventral to the nasal septum and medial to the anterior tips of the posterior paraseptal cartilages. At this early stage they bear no intimate relations to the posterior paraseptal cartilages but in the 17 mm stage previously described the vomer has already commenced invasion of the latter cartilages.

G. THE PTERYGOID

in the 17 mm embryo of Elephantulus conforms in general structure to the pterygoid in the 9.5 mm embryo of Suncus. The pterygoid cartilage is massive and it forms by far the greater part of the pterygoid at this

VOL 28 194

stage. Compared to Suncus the hamulus of the pterygoid, which at this stage is also entirely cartilaginous, is much more massive in Elephantulus (fig. 35). The posterior osseous portion of the pterygoid is only very small in this young embryo and it has the form of a bony rod rather than a bony plate. This bony portion of the pterygoid in Elephantulus does not bear any intimate relations with the pterygoid process of the ala temporalis. During the later stages of its development, however, the pterygoid does invade the pterygoid process of the ala temporalis, although this does not take place on the same scale as in Suncus.

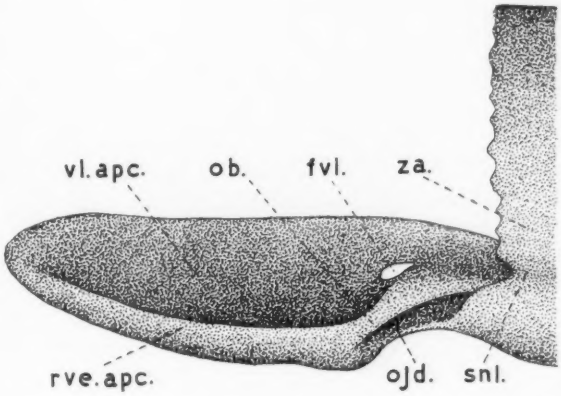

Fig. 36. Lateral view reconstruction of the anterior paraseptal cartilage of a 17 mm embryo (× 40).

The first signs of chondrification in the pterygoid were observed in the 14.1 mm embryo. At this stage the anterior end of the blastematous pterygoid bone displays very intimate relations with the posterior extremity of the palatine. In the 15.3 mm embryo conditions were found to be much similar although definite signs of an ossification appearing in the posterior extremity of the pterygoid cartilage could be observed. From this point the ossification was found to spread backwards along a dense strand of blasteme in true dermal bone fashion, but as in Suncus this posterior osseous portion of the pterygoid was found not to arise from an autogenous centre but to develop in continuity with the pterygoid cartiage. The thicker anterior portion of the pterygoid, both in Suncus and Elephantulus, is therefore preformed in cartilage while its posterior portion, although it does not arise from a separate centre, has a dermal bone character from the start. DE BEER (1929, p. 451) gives a long list of Mammals in which the pterygoid cartilage has been found and, except for Monotremes, this cartilage seems to be more or less characteristic for Mammals. The latter author, however, as also FAWCETT (1905) and GAUPP (1901) does not question the secondary nature of the pterygoid cartilage so that it cannot be homologized with primary cartilage. It represents the preformation of a dermal bone just as the nodules of secondary cartilage in the palatine processes of the maxilla, premaxilla, palatine, dentary etc.

Judging from the material at my disposal the double origin of the Mammalian pterygoid, as maintained by LUBOSCH and DE BEER could not be confirmed. The latter author (1929) maintains that the pterygoid in the 11 mm

embryo of Sorex is composed of two elements, viz. a cartilaginous portion which he homologizes with the Reptilian pterygoid and a dermal bone portion, which he regards as the homologue of the basitemporal (= detached lateral wing of the parasphenoid). Already at this early stage DE BEER reports the connection of this latter dermal bone "with the ossification which is beginning to set in in the pterygoid cartilage at the point of fusion of the latter with the pterygoid process of the ala temporalis (p. 432). He does not, however, mention the earliest development of these two elements of the pterygoid which at this stage were already fused. The condition prevalent in the young embryo of Suncus (9.5 mm) conforms in detail to the condition described by DE BEER for Sorex, but the earliest development of the elements concerned does not justify their derivation from entirely different elements in Reptiles. I shall refrain from discussing the already much disputed problem of the possible homologies of the Mammalian pterygoid and the "pterygoid elements" found in Monotremes for a review of which the reader is referred to DE BEER (1929) and STADTMÜLLER (1936). Sufficient to state that, as far as Suncus and Elephantulus are concerned, the persisting pterygoid element, judging from its relations to neighbouring structures and especially to the palatine, basisphenoid and alisphenoid, seems to combine the relations borne by both Monotreme elements. It is therefore possible that LUBOSCH and DE BEER may be correct in their conjecture of the possible double origin of the Mammalian pterygoid, in which case the Mammalian ontogeny supplies but very little information.

H. THE NASALS,

in the 17 mm embryo of Elephantulus, display similar relations to neighbouring structures as the same elements in the 18.3 mm embryo of Suncus, with the only exception that they do not extend quite as far back and are not fused in the mid-dorsal line, neither do they fuse with each other at a later stage of their development. The junction between the nasals and frontals in the adult Elephantulus has the form of a transverse rather than a V-shaped suture, although the postero-lateral edge of each nasal projects slightly further back than its postero-medial edge. This results in the formation of a suture which has the shape of a very wide "V" with the apex directed forwards.

In Elephantulus the nasal first appears shortly after the 15.3 mm stage, but due to the lack of an intermediate embryonic stage I was unable to determine whether or not it arises from a single centre, although this seems to be the more likely.

I. THE FRONTAL

in the 17 mm embryo of Elephantulus is much more massive than in Suncus. It is a thick bone with the anterior and ventral edges highly pneumatic. The

VOL 28 194

postero-lateral tip of the frontal is slightly overlapped by the parietal but it is not fused with the latter bone and neither does it fuse with the parietal at a later stage of its development. The upper edge of the cartilaginous commissura sphenethmoidalis is fused with the inner surface of the frontal over a short distance. The frontal, even in the adult skull, does not show the slightest indication of a postorbital process. The orbital division of the frontal is fairly extensive in the adult skull. Bordered by the orbital divisions of the frontal, the parietal and the upper edge of the alisphenoid a large foramen for the transmission of a vein is isolated. The frontal retains its separate identity throughout life, and even the sutura frontalis or metoptica is not obliterated as is usually the case in Insectivores.

The frontal first appears in the 12.2 mm embryo lying antero-lateral to the extreme anterior tip of the bulbus olfactorius. It arises from a single centre as in Suncus.

VOL. 28 1947

J. THE PARIETAL

in the 17 mm embryo of Elephantulus presents very little of particular interest. As in the 18.3 mm Suncus embryo the two parietals do not meet each other in the mid-dorsal line while ventrally they reach the upper border of the temporal portion of the squamosal. The anterior ventro-lateral portion of the parietal is highly pneumatic. During the later stages of their development the extensive parietals meet the frontals, alisphenoids, squamosals and interparietal but they do not fuse with any of these elements. The saggital suture between the two parietals is also retained throughout life.

The parietal ossification first appears in the 13.5 mm embryo of Elephantulus. At this early stage the parietal has the shape of an extremely thin and much perforated bony plate so that in section it is rather difficult to determine whether it arises from a single centre or from a number of concentrated centres.

K. THE SQUAMOSAL

in the 17 mm embryo of Elephantulus displays only a poorly developed glenoid cavity. Dorso-lateral to this cavity it bears a short but well developed zygomatic process which participates in the formation of the posterior part of the zygomatic arch and which, already at this early stage, articulates with the postero-dorsal aspect of the jugal. The temporal portion of the squamosal at this stage does not extend quite as far back as the primary stylomastoid foramen and its upper edge nearly reaches the ventral border of the parietal. During the later stages of its development the temporal portion of the squamosal greatly expands and extends as far back as the antero-lateral border of the interparietal, no part of the periotic being exposed between the squamosal and the parietal. Between the latter two bones, however, a well defined for-

amen for the transmission of a large vein is retained. The lower border of the temporal portion of the squamosal takes part in the formation of the dorso-lateral covering for the middle ear. At no stage of its development does the glenoid cavity on the squamosal display a well defined processus postglenoideus. Even in the late embryonic stages the alisphenoid was found still to participate in the formation of the extreme ventral division of the glenoid cavity. Although it was somewhat difficult to determine sutures in this region of the adult skull it is quite possible that this condition may be retained in the adult. The extreme postero-ventral tip of the pars entoglenoidea squamosi, in the 30 mm embryo, takes very little part in the formation of the osseous bulla but it is quite possible that during the later stages of development this latter part of the squamosal may expand into a small processus tympanicus squamosi.

The squamosal ossification was first observed in the 13.5 mm embryo of Elephantulus. At this stage the ossification already comprises a minute spur representing the future zygomatic process and a small flat glenoid portion so that the ossification centre of the squamosal must be somewhere near the base of the zygomatic process.

VOL
28
194

L. THE TYMPANIC (ECTOTYMPANIC),

in the 17 mm embryo of Elephantulus, has the characteristic C-shape with the ventral postero-medial limb much longer than the dorsal antero-lateral limb so that the deficiency in the tympanic ring is directed postero-dorso-laterally. The relations to neighbouring structures is about the same as in Suncus. In the oldest embryonic stage of Elephantulus that I had at my disposal, viz. a 34 mm embryo, the tympanic bone still had the typical C-shape so that it was not possible to determine its final shape in the adult.

The centre for the tympanic ossification could be observed for the first time in the 15.3 mm embryo.

M. THE GONIAL (PREARTICULAR),

in the 17 mm embryo of Elephantulus displays relations not unlike those described for the Suncus embryo of 18.3 mm and at this early stage it is already fused with the malleus. In the later stages the gonial greatly increases in size and apart from the chorda tympani the foramen through the gonial also transmits a fairly large vein.

This bone in Elephantulus develops in true dermal bone fashion and first appears in the 15.3 mm embryo.

N. THE INTERPARIETAL

in the 17 mm embryo of Elephantulus is a C-shaped bone lying anterior to the supraoccipital cartilage and partly overlapping the anterior border of

this cartilage. During the later stages of its development the interparietal becomes inseparably fused with the supraoccipital ossification but it always remains demarcated from the parietals by a well defined suture. In Elephantulus two definite lateral ossification centres could be distinguished in the interparietal. These centres first appear in the 14.1 mm embryo.

V. SUMMARY.

The following points in the development of the chondrocranium and early osteocranium of Elephantulus are noteworthy:

a. *The central stem.*

1. The central stem at the optimal stage of chondrification is almost straight but it displays a pronounced cephalic flexture during the early embryonic stages.
2. The fenestra hypophyseos is obliterated at a very early stage, being entirely absent even in the late blastematous lamina hypophyseos.
3. The alicochlear commissures are well defined.
4. The fossa hypophyseos is defined and a low dorsum sellae is present.
5. The lamina hypophyseos is exceptionally wide.
6. The demarcation between the trabecular plate and the lamina hypophyseos is retained until after the 10.5 mm stage but the lamina hypophyseos and basal plates fuse at a very early stage of development.
7. The fissura basicochlearis develops very early in ontogeny being well defined in blasteme.
8. The notochord forms a transitional stage between the retrobasilar and basilar types (TOURNEUX).
9. No traces of paired "polar elements" could be detected in the development of the lamina hypophyseos.
10. No mesethmoid ossification could be distinguished.
11. The presphenoid ossifies separately from two centres but soon fuses with the orbitosphenoids.
12. The basisphenoid and basioccipital each ossifies from a single centre, the centre for the basioccipital being situated a short distance anterior to the incisura intercondyloidea.
13. A processus tympanicus basisphenoideae is either absent or ill-defined.

b. *Exoccipital cartilages.*

1. Only one pair of hypoglossal foramina is present.
2. The lamina alaris is present but not fused with the commissura occipito-capsularis posterior so that a fissura occipito-capsularis inferior is retained.

3. The exoccipital cartilages arises from definite autogenous chondrification centres.
4. The lamina alaris chondrifies fairly late.
5. The connection of the lamina alaris with the otic capsule is never very intimate and the processus paracondyloideus is poorly developed.

c. *Auditory capsule.*

1. The convergence of the two cochlear capsules antero-ventrally is pronounced.
2. A long undivided basicochlear fissure is present.
3. Both superior and inferior occipito-capsular fissures are present these being separated by a well defined posterior occipito-capsular commissure.
4. The parietal plate is poorly developed. It is connected with the otic capsule and supraoccipital but not with the ala orbitalis.
5. An opercular process is absent.
6. The tegmen tympani is conspicuous.
7. The crista parotica is massive.
8. The suprafacial commissure is strongly developed and a secondary facial foramen is absent.
9. The infero-medial surface of the pars canalicularis displays a large fossa subarcuata inferior interna.
10. The recessus supra-alaris is narrow.
11. A processus tympanicus petrosi caudalis is present.
12. A foramen (canalis) singulare is present.
13. A separate foramen for the lower saccular nerve is isolated fairly late in ontogeny.
14. The foramen endolymphaticum is long and slit-like.
15. The fenestra ovalis and rotunda display usual relations.
16. The constituent parts of the fissura metotica, (viz. apertura medialis and jugular foramen) are not demarcated, consequently still showing primitive relations.
17. The commissura basicochlearis posterior is extremely narrow.
18. The processus recessus develops fairly late in ontogeny.
19. The processus tympanicus petrosi caudalis is preformed in cartilage and chondrifies in continuity with the otic capsule.
20. The otic capsule ossifies from two main centres.
21. A separate ossification centre could be distinguished in the tympanohyale.
22. The processus tympanicus petrosi caudalis greatly increases in size during the later embryonic stages and it ossifies very late and in continuity with the otic capsule.

VOL
28
194

23. A small rostral entotympanic is present but during the later developmental stages it becomes inseparably fused with the horizontal caudal plate of the cartilago tubae and auditivae.
24. A separate caudal entotympanic is absent.
25. It is concluded that the caudal petrosal plate of Elephantulus may be of a double homology, including both a caudal entotympanic and a real processus tympanicus petrosi caudalis.

d. *The ala temporalis.*

1. The antero-lateral process of the ala temporalis displays only an incisura ovalis.
2. The antero-lateral process is slightly bifurcated.
3. A foramen alisphenoidale for the transmission of the arteria infraorbitalis is present.
4. The pterygoid process is very long and nearly reaches the pterygoid cartilage.
5. At its optimal stage of development the pterygoid process is not invaded by the pterygoid bone.
6. The ala temporalis is joined to the central stem and cochlear capsule by the processus alaris and alicochlear commissure respectively.
7. The ala temporalis chondrifies from an autogenous centre.
8. The processus pterygoideus chondrifies fairly late and arises from an autogenous centre.
9. The alisphenoid ossifies from a single centre which is situated lateral to the foramen alisphenoidale.
10. Late in ontogeny the pterygoid bone invades the pterygoid process of the ala temporalis and becomes inseparably fused with the alisphenoid.
11. A poorly developed processus tympanicus alisphenoideae is present in late embryonic stages.
12. A crista lateralis bullae alisphenoideae is present, the lateral surface of which participates in the ventral delimitation of the glenoid cavity.

e. *The ala orbitalis.*

1. The ala orbitalis is massive.
2. The extensive pre- and postoptic roots of the ala orbitalis join the trabecular plate separately.
3. The ala hypochiasmata is absent at the optimal stage of chondrification of the ala orbitalis, but it is recapitulated in early ontogeny.
4. The orbito-parietal commissure is deficient.
5. An anterior clinoid process is absent.
6. The upper edge of the ala orbitalis is invaded for some distance by the inner aspect of the frontal bone.

7. The ala orbitalis chondrifies from an autogenous centre but fuses with the central stem at a relatively early stage of its development.
8. The orbitosphenoid ossifies from a single centre situated antero-lateral to the large optic foramen.

f. *The supraoccipital cartilage.*

1. The supraoccipital cartilage is extensive.
2. It bears no structure capable of identification with the so-called "opercular process" of FAWCETT.
3. The supraoccipital cartilage arises from a single centre in the mid-dorsal line.
4. The supraoccipital bone ossifies from two lateral centres which soon fuse with each other.
5. Fusion between the supraoccipital and interparietal takes place in late ontogeny.

VOL
28
194

g. *Membrane bones.*

1. The maxilla displays a well developed processus extranasalis and processus palatinus medialis.
2. The palatine process of the premaxillae do not fuse with each other at any stage of their development.
3. The whole premaxilla, including the processus palatinus medialis, ossifies from a single centre.
4. The infraorbital foramen pierces the maxilla and the lacrimal bone does not take part in its formation.
5. The zygomatic process of the maxilla is well developed and it joins the jugal.
6. The maxilla ossifies from a single centre and displays a small but well defined nodule of secondary cartilage in its frontal process.
7. The hard palate is rendered most incomplete by several sets of huge elongated fenestrae in the palatal divisions of the maxillae and palatines.
8. The lacrimal bone is pierced by the lacrimal canal and it bears a long postero-laterally directed spur which joins the jugal.
9. The zygomatic arch is complete and the jugal participates in its formation.
10. The jugal does not display an extensive foramen malare.
11. The palatine ossifies from a single centre which occupies the same position as in Suncus.
12. The vomer invades the posterior paraseptal cartilages and laminae transversales posteriores at an early stage of development and later becomes inseparably fused with the ethmoid.
13. The vomer ossifies from paired lateral centres.
14. The pterygoid cartilage is massive.

15. The hamulus of the pterygoid is strongly developed.
16. The pterygoid develops from a single centre.
17. The two nasals retain their separate identity throughout life.
18. The junction between the nasals and frontals has the form of a transverse rather than a V-shaped suture.
19. The frontals are massive with the anterior and ventral edges strongly pneumatic.
20. The postorbital bar is deficient and the frontal shows no indication of a processus post-orbitalis.
21. The frontals retain their separate identity throughout life.
22. The parietals also retain their separate identity throughout life.
23. The squamosal displays a well developed zygomatic process.
24. The processus postglenoideus of the squamosal is poorly developed.
25. The possible presence of a small processus tympanicus squamosi in the adult skull is not excluded.
26. The squamosal ossifies from a single centre near the base of its zygomatic process.
27. The tympanic (ectotympanic) bone has the characteristic horseshoe shape in ontogeny but its final shape could not be determined through a lack of juvenile material.
28. The gonial (prearticular) shows its usual relations and is pierced by a foramen for the chorda tympani and a vein.
29. The interparietal fuses with the supraoccipital but remains distinct from the parietals.
30. The interparietal ossifies from paired lateral centres.

OL.
28
947

PART III. EREMITALPA GRANTI (BROOM).

I. INTRODUCTION.

The systematic position of the Golden Moles has been of great uncertainty in the past. Classically they were included in the Insectivore Order and more particularly in HAECKEL's "Lipotyphla". This systematic position, however, was by no means settled as has been admitted by most systematists in the past.

The adult comparative anatomy of this problematic group gives some information regarding their affinities but this information is often more misleading than helpful because these nocturnal burrowing animals are so markedly adapted in various respects to their specialized habits, that one has to be constantly on the alert against attaching too much phylogenetic significance to mere secondary modification. Only the palaeontology and comparative em-

bryology of the group remain, therefore, whereby the problem of their true affinities can be settled. Of their palaeontology nothing is known and therefore the onus rests mainly on the comparative embryology to settle this dubious question.

Our knowledge of the Chrysochlorid embryology, however, is likewise sadly deficient, and this is undoubtedly due to the comparatively limited distribution of these animals and the difficult task of collecting embryonic material. Up till now only the later stages of development of the skull of these animals have been studied (BROOM 1915 and 1916), and that study was by no means exhaustive, since BROOM had only two specimens available; one of a newly born *Chrysochloris hottentotta* and another of a slightly older *Chrysochloris asiatica*. COOPER (1928) also investigated the ear region of a late foetus of *Chrysochloris asiatica*. These investigations did not solve the mystery enveloping the true Chrysochlorid affinities, but merely cast doubt on the classical retention of this group in the Lipotyphla and drew attention to some remarkable features in its cranial morphology, which, however, could not be accounted for without a study of further embryonic material. BROOM (1916), however, came to the following interesting conclusion: "the examination of the skull confirms the result of the examination of Jacobson's organ and its relations (1915 a, b), in showing that Chrysochloris is not a near ally to Centetes, and that it is not an Insectivore. Further, it is not allied to the Menotyphla and ought to be placed in a distinct order Chrysochloridae" (p. 458). This view expressed by BROOM has not been generally accepted by systematists in the past.

This present investigation into the depelopment of the chondro- and osteocranium of the Golden Moles has been undertaken in order to contribute to our knowledge of the embryology of the group, and along that way to endeavour to shed new light on the true affinities of the Chrysochloridae.

Eremitalpa granti, used for the present investigation has been described first by BROOM (1907) as *Chrysochloris granti*. His material consisted of four skulls collected in 1898 at Garies, Namaqualand, from the disgorged pellets of owls. In 1909 BROOM added further details, obtained from a spirit specimen found in the South African Museum, to his original description of the species.

AUSTIN ROBERTS (1923) revised the generic arrangement of the Chrysochloridae and established eight separate genera. *Chrysochloris granti* BROOM was subsequently transferred to the newly established genus *Eremitalpa* of which it formed the only known species.

II. MATERIAL AND TECHNIQUE.

The Embryonic material of *Eremitalpa granti* was collected mainly at Port Nolloth, North-western Cape Province, and fixed in Bouin solution.

VOL
28
194

The heads of the older embryos were decalcified in Ebner's solution, neutralized, dehydrated and embedded in paraffin wax. Serial sections were cut at a thickness ranging from 10 μ in the younger to 15 μ in the older embryonic stages. The section were stained on the slides with Hansen's Haematoxylin and Eosin.

The following measurements of the Eremitalpa embryos were taken from the tip of the snout, round the mid-dorsal curvature to the vent: 18 mm; 21 mm; 24 mm; 25 mm; ± 27 mm; 28.5 mm; 28.5 mm; 31 mm; 36 mm; 41 mm and 45 mm.

The one 28.5 mm embryo was sectioned longitudinally, and a median sagittal section of this embryo supplied a very accurate baseline for a lateral view graphic reconstruction of the chondrocranium of the other 28.5 mm embryo, which was sectioned transversely. At this latter stage the chondrocranium was found to have obtained more or less its optimal stage of development.

VOL. 28 1947

III. THE CHONDROCRANIUM.

The Chondrocranium of the Golden Mole, like the adult skull, is striking for its relatively short but very wide outline, this being due to the large size of the brain cavity; the facial region being short and narrow. BROOM (1916) also noticed this, regarding the skull as bearing "a slight superficial resemblance to that of a small bird" (p. 450).

FAWCETT'S (1917) method of describing the chondrocranium will chiefly be followed in this paper. This author subdivided the chondrocranium into: A, the central, stem; B, its appendages; C, lateral structures; D, the commissures interconnecting these and E, the dorsal structures.

A. THE CENTRAL STEM.

Morphologically the central stem is made up of: (I) A chordal region, also known as the parachordal plate or planum basale; (II) A prechordal region which in Mammals usually arises in two parts viz. a. The trabecular plate (pars Interorbitonasalis of FAWCETT) b. The lamina hypophyseos (pars Trabecularis of FAWCETT). At the stage of optimal chondrification of the primordial cranium in Eremitalpa the regions of the central stem are completely fused with each other and the passage from one region to another is gradual. The central stem forms a pronounced curve with its concavity directed downwards and its maximal concavity lying opposite the hind end of the nasal capsule. This pronounced curve in the central stem is in sharp contrast to the condition prevalent in other Insectivores in which the relatively straight central stem seldom failed to arouse comment. A condition not very

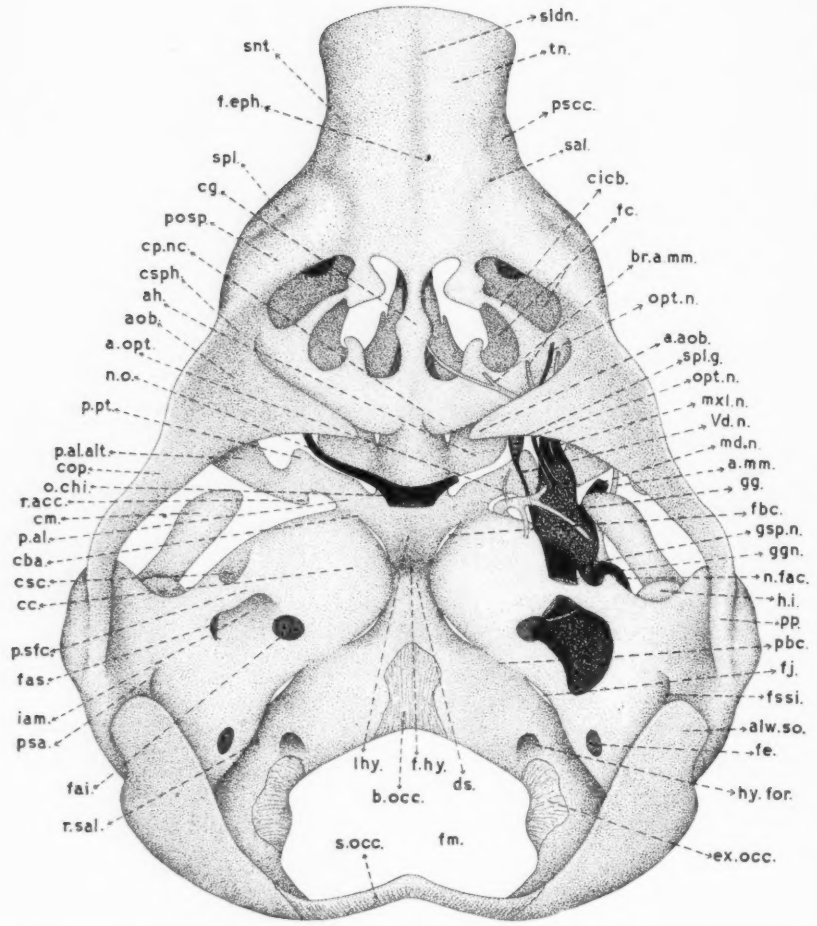

Fig. 37. Dorsal view reconstruction of the chondrocranium of a 28.5 mm embryo, showing also the relations of some important nerves and bloodvessels (× 20).

unlike that found in Eremitalpa is encountered in the earlier embryonic stages of Elephantulus. Opposite the dorsum sellae the central stem in Eremitalpa displays a marked ventrally directed convexity.

The planum basale (figs. 37, 38), which is roughly triangular in shape, has a very wide and thin base which is almost flat and which forms the anterior delimitation of the foramen magnum. The hypoglossal foramina, of which only a single pair is present, and the jugular foramina delimit the base of the triangular basal plate from the pila occipitalia and the posterior part of the cochlear capsule respectively. The apical portion of the basal plate is extremely narrow, thick and rod-like in section, being compressed to a remarkable extent by the pronounced medial extension of the cochlear capsules. In

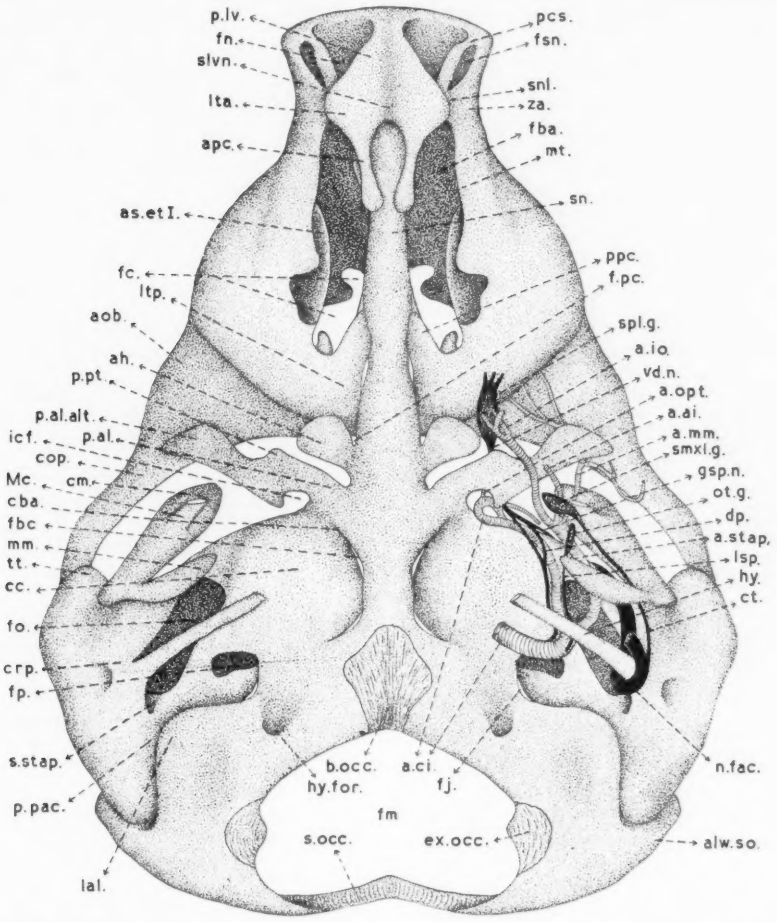

Fig. 38. Ventral view reconstruction of the chondrocranium of a 28.5 mm embryo, showing also ossification centres and the relations of some important vessels and nerves (× 20).

this respect it closely resembles Tupaia (HENCKEL 1928) and Elephantulus. The apical portion of the basal plate is separated from the cochlear capsule by a well-defined but extremely narrow and strongly medially curved basicochlear fissure. The posterior basicochlear commissure (chordo-cochlear commissure of FAWCETT), binding the basal plate to the cochlear capsule, is well developed.

At this stage of development no trace of the chorda dorsalis is left in the region of the planum basale.

The lamina hypophyseos (figs. 37, 38), in Eremitalpa is exceptionally short and very wide so that the carotid foramina are placed very far laterally. No trace of the fenestra hypophyseos is left at this stage of development. The

lateral margin of the short lamina hypophyseos bifurcates into the processus alaris anteriorly and the anterior basicochlear commissure (posterior trabeculo-cochlear commissure of FAWCETT) posteriorly. The processus alaris fuses with the ala temporalis and gives off a short posteriorly directed spur lateral to the internal carotid artery. This little spur represents the only rudiment of the alicochlear commissure which is deficient in its posterior part. The carotid foramen, thus, is not bound laterally by a complete alicochlear commissure as is usually the case in mammals, with the exception of the higher Primates. The anterior basicochlear commissure is fused with the anterior end of the cochlear capsule and delimits the carotid foramen from the basicochlear fissure.

The fossa hypophyseos in Eremitalpa, compared with other Insectivores, is well defined. This is due to the presence of an appreciable dorsum sellae, although a tuberculum sellae could not be distinguished (fig. 39).

The trabecular plate in Eremitalpa has the shape of a short and thick rod in its posterior part where it is continuously blended with the lamina hypophyseos. Anterior to the orbito-nasal fissures it gains rapidly in dorso-ventral thickness becoming the septum nasi which will be described in detail with the nasal capsule. The only lateral appendages of the posterior part of the pars trabecularis are the extensive wing-shaped alae hypochiasmatae—the pre- and post-optic roots of the ala orbitalis being deficient.

1. Early Development of the Central Stem: Up to the 21 mm stage the central stem is entirely blastematous. At this stage the dense concentration of blastem representing the precursor of the pars trabecularis is separated from the future lamina hypophyseos by a strand of relatively undifferentiated mesenchyme. The lamina hypophyseos is represented in blastem by a cell concentration on either side of the canalis craniopharyngeus. Posteriorly these cell concentrations (polar elements) are in direct continuity with the blastematous planum basale, the latter being separated from the blastematous auditory capsule by a well-defined basicapsular fissure on either side. The planum basale is furthermore in slight continuity with blastem centres of the exoccipitals. No trace of a fenestra basicranialis posterior or paired parachordal elements can be distinguished in the blastematous planum basale. The anterior end of each "polar element" is in slight continuity with the dense blastem concentration of the ala temporalis through the ill-defined processus alaris.

In the 24 mm embryo the posterior part of the pars trabecularis is slightly chondrified, its anterior part being still procartilaginous and even blastematous in its extreme anterior tip. At this stage the pars trabecularis is already in strong procartilaginous continuity with the lamina hypophyseos; it does not, however, establish cartilaginous continuity with the alae hypochiasmatae before the 27 mm stage.

VOL
28
194

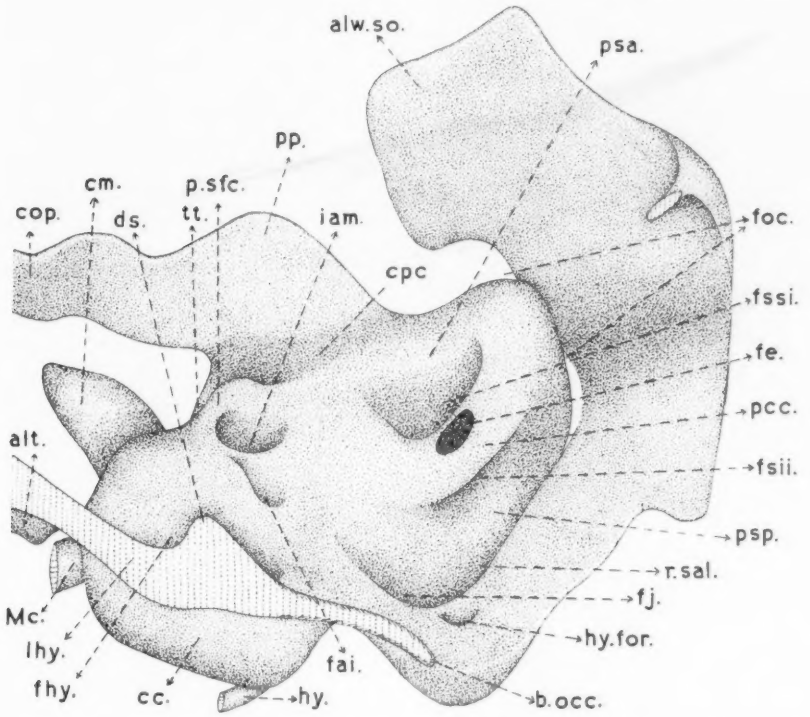

Fig. 39. Medial view reconstruction of the occipital and otic regions of the chondrocranium of a 28.5 mm embryo (× 30).

The lamina hypophyseos in the 24 mm embryo is a continuous, slightly chondrified, plate which does not show any polar elements or a fenestra hypophyseos. This very early obliteration of the fenestra hypophyseos reminds one of the condition prevalent in Elephantulus.

Posteriorly the lamina hypophyseos is continued into the planum basale. The anterior basicochlear commissure is still deficient at this stage and is not defined in cartilage until in the 27 mm stage.

Antero-laterally the lamina hypophyseos communicates with the slightly chondrified ala temporalis through the procartilaginous processus alaris, this connection being already cartilaginous in the 25 mm embryo. The alicochlear commissure, which in the Golden Mole does not appear at any later stage of development, is not even preformed in blastem. In the 24 mm embryo its anterior part is defined in blastem, but this rudiment does not extend as far back as the cupula anterior of the cochlear capsule. In this respect, therefore, the Golden Mole, although primitive in many other respects, has to be regarded as rather specialized.

The alicochlear commissure representing either the entire posterior end of

the trabecula (DE BEER) or merely a developmentally retarded postero-lateral portion of the trabecula, is as a rule recapitulated in the ontogeny of Mammals, being only constantly absent in Primates. In the Golden Mole the internal carotid arteries are therefore completely extra-trabecular, even in the earliest stages of the development of the chondrocranium, as is the case also in Primates.

The planum basale in the 24 mm embryo is fairly well chondrified being continuous with the lamina hypophyseos in front and with the exoccipitals behind. It is separated from the cochlear capsule by a well-defined basicochlear fissure. The posterior basicochlear commissure is well defined in procartilage and is already chondrified in the 25 mm embryo. Towards its middle the planum basale displays a pair of small deficiencies, one on either side of the mid-line. In the 25 mm embryo these deficiensies are obliterated, being filled up with thin cartilage. Their significance is obscure but they may represent the remains of a once more extensive posterior basicranial fenestra.

The relations of the notochord to the planum basale are of interest. In the earliest stages of development, while the planum basale is still blastematous, the notochord lies dorsal to it. When chondrification sets in, however, the anterior part of the notochord becomes embedded in the basal plate while its posterior part remains superficial (dorsal) to the basal plate. A similar condition has been reported for Elephantulus and for the sheep (BOLK 1922), the latter author regarding this condition as intermediate between his intrabasilar and transbasilar types. The cranial part of the notochord in Eremitalpa is resorbed at a relatively early stage. In the 27 mm embryo its middle portion is resorbed while in the 28.5 mm embryo it was found to be completely resorbed.

2. Post optimal changes in the central stem: As a rule the central stem is taken to ossify in four parts, viz. a mesethmoid and presphenoid in the pars trabecularis; a basisphenoid in the lamina hypophyseos and a basioccipital in the planum basale. Up to the latest embryonic stage investigated by the author, viz. a 45 mm embryo, only the last mentioned two ossifications could be made out; whether a presphenoid and mesethmoid occur at any later stages of development could therefore not be determined.

Some light is thrown on this matter, however, by investigations by BROOM (1927) into this region of a young specimen of *Chrysochloris asiatica*, in which he could distinguish only a well-marked presphenoid ossification, replacing the mesethmoid. There is good reason to believe that this represents the condition prevalent in all members of the Chrysochloridae.

The basioccipital ossification in Eremitalpa first appears in the 28.5 mm embryo, where, although fairly extensive, it has only the character of a perichondral ossification. It arises from a single centre in the planum basale a short distance anterior to the incisura intercondyloidea. In the 45 mm stage the basioccipital is still separated from the basisphenoid and exoccipitals by

intervening strips of cartilage. The posterior part of the basicochlear fissure between the basioccipital and auditory capsule is still wide and the lower anterior tip of the occipital condyle is formed by the basioccipital.

The basisphenoid makes its first appearance as a perichondral ossification of the lamina hypophyseos in the 31 mm embryo. Already in the 36 mm embryo it displays a pair of small tympanic processes medial to the cupulae anteriores of the cochlear capsules. In the 45 mm stage the basisphenoid is still separated from the alisphenoids and from the basioccipital by intervening strands of cartilage but it extends rather far forwards, well into the presphenoidal region, where it is interposed between the two orbitosphenoids, establishing intimate relations with these. At this stage the basisphenoid bears a pair of conspicuous wing-like processes (fig. 41). These processes spring from the ventro-lateral aspect of the basisphenoid and project forwards, downwards and laterally. Each contributes to the formation of the medial wall of the postero-ventral part of the osseous bulla. BROOM (1916) recognised this wing of the basesphenoid in a young specimen of *Chrysochloris hottentotta* and regarded it as comparable to the basisphenoidal process of many reptiles in having a true articulation with the pterygoid. VAN DER KLAAUW (1929) reported a fairly well developed processus tympanicus basisphenoidei in an unnamed species of Macroscelides. KEEN and GROBBELAAR (1941) also mentions an extensively inflated basisphenoid in *Macroscelides probiscideus* while WEBER (1928) regards the presence of a processus tympanicus basisphenoidei as characteristic of the Insectivores.

B. LATERAL STRUCTURES APPENDED TO THE CENTRAL STEM.

These include the exoccipital cartilages; the auditory capsule; the alae temporales; the alae orbitales and the nasal capsules. (The foramina intervening between these lateral structures and the central stem will be discussed with the structures concerned.)

1. The Exoccipital Cartilage (figs. 39 and 40) in Eremitalpa is fused below with the postero-lateral angle of the planum basale. The hypoglossal foramen which indicates the site of union lies behind and slightly medial to the jugular foramen (fig. 37). The lamina alaris of the exoccipital is well-defined and its anterior edge is closely applied to, but not fused with, the ventro-lateral aspect of the pars canalicularis of the otic capsule behind the jugular foramen. The processus paracondyloideus is inconspicuous and the recessus supraalaris, although well-defined, is rather narrow and leads postero-dorsally into the much compressed lower end of the fissura occipito-

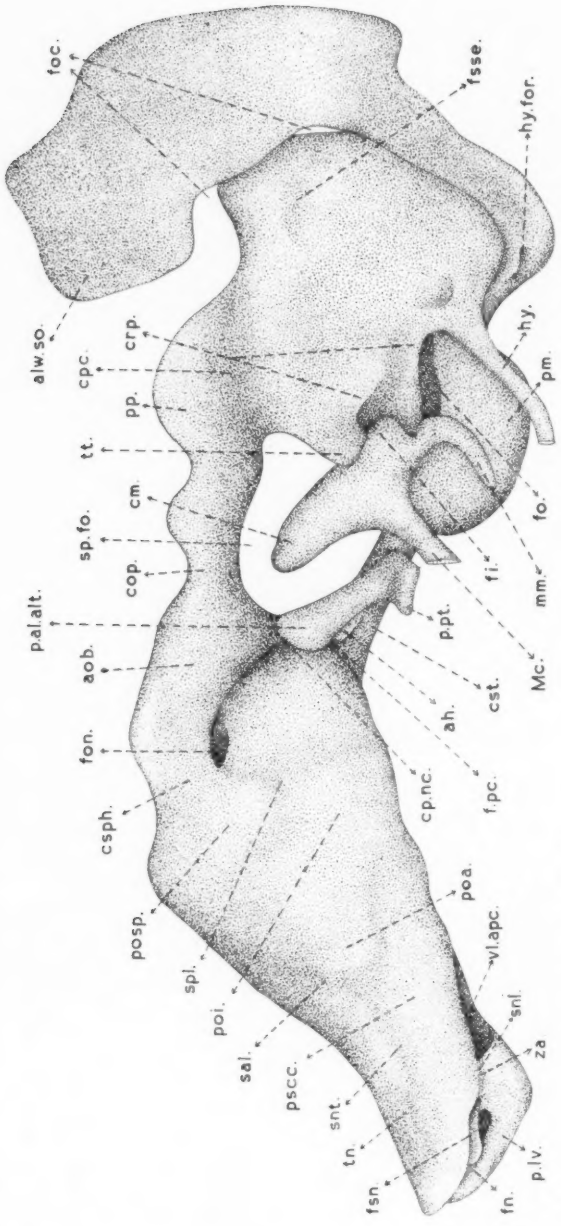

Fig. 40. Lateral view reconstruction of the chondrocranium of a 28.5 mm embryo (× 25).

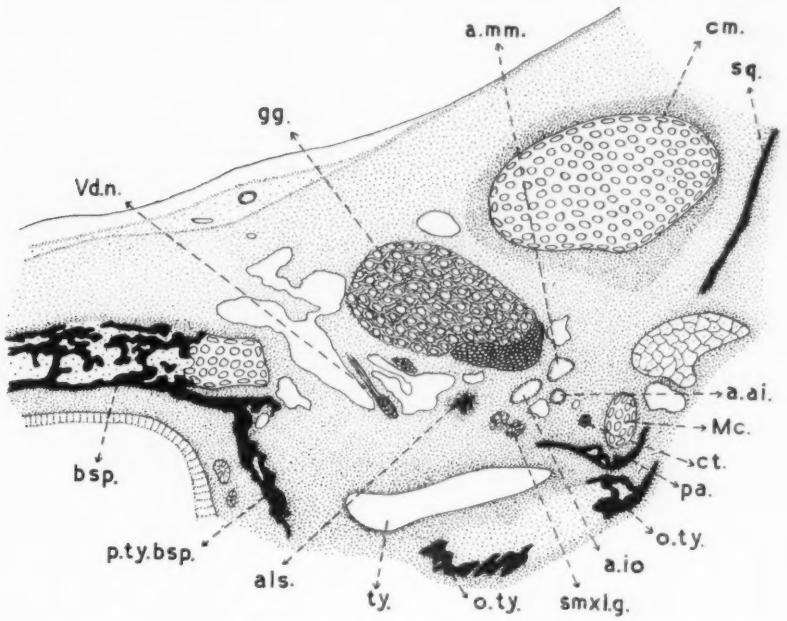

Fig. 41. Transverse section through basisphenoidal region of the base of the skull of a 45 mm embryo of Eremitalpa granti, in order to illustrate the relations of the processus tympanicus basisphenoidei (× 30).

capsularis. The posterior occipito-capsular commissure is absent so that the superior and inferior occipito-capsular fissures are confluent.

Superiorly the exoccipital cartilage merges into the supraoccipital cartilage, but, due to the absence of the parieto-occipital commissure, the occipital cartilages have no direct communication with the parietal plate and consequently the occipito-capsular fissure is not bound by cartilage antero-superiorly. The occipital condyles are rather ill-defined at this stage of development.

a. *Early development of the exoccipital cartilage:* In the earliest stages investigated (18 and 21 mm) the exoccipital is completely blastematous and in the 21 mm stage it displays a well-defined autogenous blastem centre which is in weak continuity with the planum basale. It chondrifies relatively early—being well chondrified and in strong cartilaginous continuity with the planum basale in the 24 mm stage. A separate chondrification centre could therefore not be made out for the exoccipital, but it seems reasonable to assume that it is present at an earlier stage but looses its separate identity very soon. In the 25 mm embryo the greater part of the lamina alaris of the exoccipital is well chondrified, but its attachment to the otic capsule is still blastematous. The exoccipital cartilage is also in weak cartilaginous continuity with the supraoccipital at this stage.

b. *Post-optimal changes in the exoccipital cartilage:* The lamina alaris does not fuse with the ventro-lateral aspect of the pars canalicularis until very late. In the 41 mm embryo this fusion is extensive and obliterates the lower end of the occipito-capsular fissure.

The first signs of perichondral ossification in the exoccipital cartilage were observed in the 28.5 mm embryo where it affects mainly the inner surface of the cartilage.

In the 45 mm embryo the exoccipital is extensively ossified but is still separated from the supraoccipital, "tabular" and basioccipital by strands of cartilage. It forms by far the greater part of the occipital condyle and at this stage it almost completely surrounds the hypoglossal foramen (fig. 44). The paracondyloid process ossifies in continuity with the exoccipital and not from a separate centre.

2. The Auditory Capsule (figs. 37—42, 39 and 42) of Eremitalpa can be divided for descriptive purposes into the pars canalicularis which lodges the semicircular canals and utricle and the pars cochlearis which lodges the saccule and the ductus cochlearis. The long axis of the auditory capsule passes obliquely upwards and backwards; the pars canalicularis being postero-dorsal in position while the pars cochlearis lies antero-ventrally. This is the case in all Mammals except Humans. The antero-ventral convergence of the two auditory capsules is pronounced and part of the cochlear capsule projects some distance below the plane of the basal plate.

The connections of the auditory capsule to neighbouring parts of the chondrocranium are briefly as follows: The pars cochlearis is attached to the lamina hypophyseos only by means of the anterior basicochlear commissure, the alicochlear commissure being deficient. It is attached to the planum basale by the commissura basicochlearis posterior. The pars canalicularis has no direct communications either with the central stem or with the occipital cartilages since the lamina alaris of the exoccipital is merely applied to its ventro-lateral aspect and the posterior occipito-capsular commissure is absent. Antero-dorsally the capsulo-parietal commissure attaches the pars canalicularis to the parietal plate.

The parietal plate is very poorly defined. It appears as a backward continuation of the orbito-parietal commissure fused by its ventral margin with the upper anterior surface of the pars canalicularis. The lateral jugular vein runs medial to the capsulo-parietal commissure and the middle meningeal artery runs backwards lateral to it. Since the occipito-parietal commissure is deficient the parietal plate has no direct communication with the occipital cartilages.

The tegmen tympani has the shape of a short blunt process which partly roofs the fossa incudis. Postero-medially it is fused with the pars canalicularis and it is continued behind into the crista parotica. The anterior end of the capsulo-parietal commissure arises from the upper aspect of the tegmen tympani.

VOL
28
194

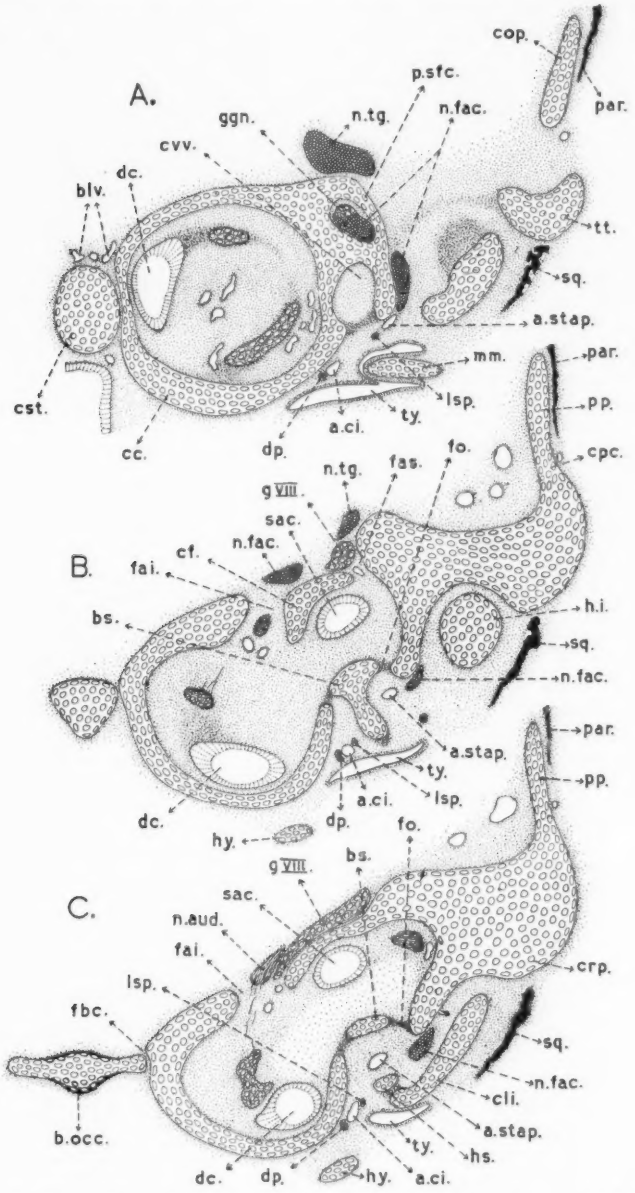

Fig. 42 A—C. Consecutive transverse sections through the anterior part of the auditory capsule of a 28.5 mm embryo (× 30).

The upper end of the tympano-hyale is fused with the ventral border of the crista parotica anterior to the primary stylomastoid foramen. Posterior to the root of the tympano-hyale the crista parotica is continued backwards as a

prominent ridge which forms a ventro-lateral covering for the sulcus musculi stapedii, thus converting this sulcus into a deep fissure. Further back the ventro-medial edge of this overhanging ridge fuses with the ventro-lateral aspect of the pars canalicularis ventral to the sulcus musculi stapedii, so that posteriorly the sulcus musculi stapedii ends in a short but blind canal.

The processus opercularis is entirely absent at this stage of development. It has thus far been described in Talpa (FISCHER (1901), NOORDENBOS (1905) and FAWCETT (1918a), Sorex (DE BEER 1929), Microtus (FAWCETT 1917) and Suncus (Author).

The medial surface of the pars canalicularis displays a well-defined fossa subarcuata superior interna, the boundaries of which are as follows: Superiorly it is bound by the prominentia semicircularis anterior; anteriorly it is bound by the prominentia utriculo-ampullaris anterior; posteriorly by the prominentia cruris communis and inferiorly by the prominentia utriculo-ampullaris posterior (inferior). The well-defined suprafacial commissure arches forwards and medialwards from the prominentia utriculo-ampullaris anterior to the antero-dorsal aspect of the cochlear capsule, thus enclosing the primary facial foramen. A secondary facial foramen is absent as in Microtus (FAWCETT 1917) and Elephantulus (Author), so that the facial nerve, after having given off the greater superficial petrosal nerve, leaves the cavum supracochleare round the anterior border of the vestibular segment to enter the sulcus facialis.

The infero-medial surface of the pars canalicularis displays the prominentia utriculo-ampullaris posterior (inferior) and an inconspicuous prominentia semicircularis posterior which partly delimit the ill-defined fossa subarcuata inferior interna from the recessus supra-alaris. Posteriorly where the prominentia semicircularis posterior ends, the two recesses merge into one another.

The lateral surface of the pars canalicularis is for the greater part uniformly convex, displaying only an inconspicuous fossa subarcuata superior externa near its posterior extremity.

The pars cochlearis can be divided into a vestibular segment which contains the saccule and a cochlear segment which contains the cochlear duct. The vestibular segment intervenes between the pars canalicularis and the cochlear segment and the foramina in its walls will be discussed later. The cochlear segment is dome-shaped with smooth convex surfaces indented by only one sulcus along its ventro-lateral aspect for the internal carotid artery and deep petrosal nerve. The cupula anterior of the cochlear segment ends behind the carotid foramen and attaches to the lamina hypophyseos by means of the anterior basicochlear commissure.

a. *Foramina in the wall of the auditory capsule:* The meatus auditorius internus lies postero-medial to the suprafacial commissure in the medial wall of the vestibular segment of the pars cochlearis. In the floor of the meatus

VOL
28
194

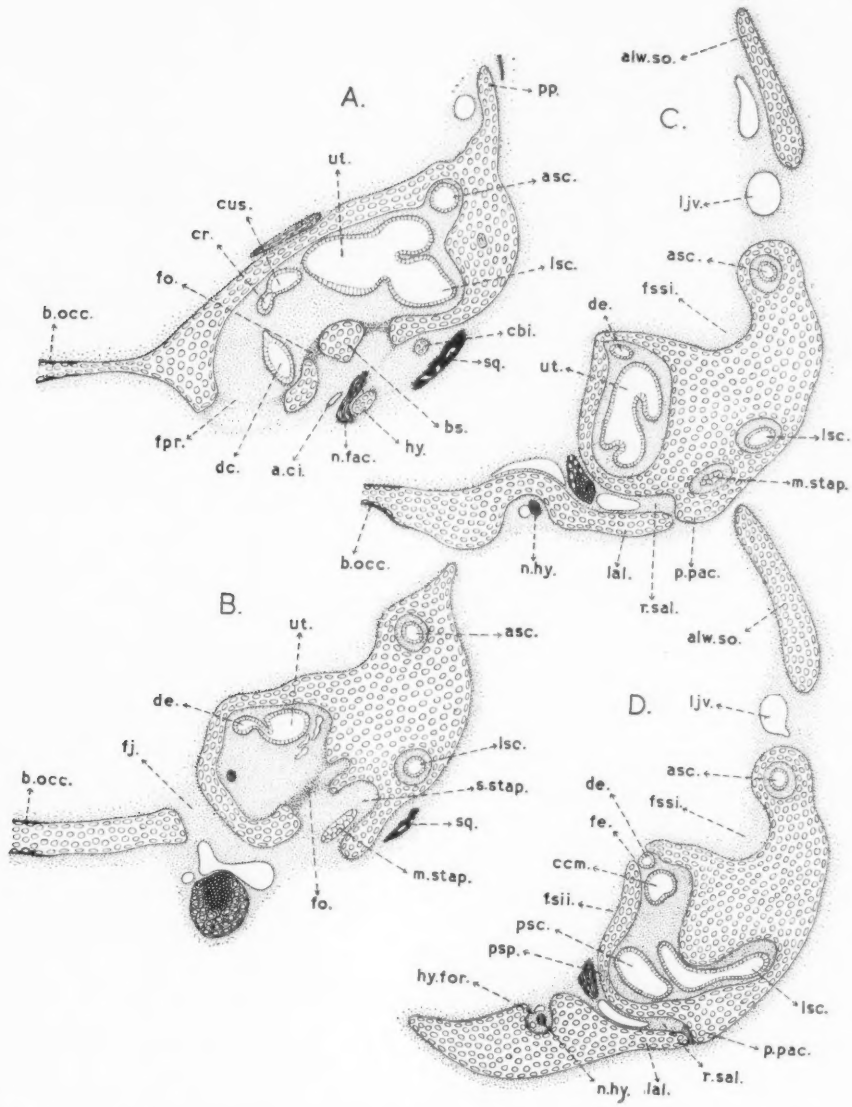

Fig. 43 A—D. Consecutive transverse sections through the posterior part of the auditory capsule of a 28.5 mm embryo (× 27.5).

are three foramina, viz. the primary facial foramen in its extreme anterior end, transmitting the facial nerve; the foramen acusticum superius and the foramen acusticum inferius, transmitting the branches of the auditory nerve, are situated postero-lateral and postero-medial to the primary facial foramen. The two latter foramina are separated by an extensive crista falciformis. At

this stage of development the foramen acusticum inferius does not display separate subdivisions either for the lower nerve to the saccule or for the nerve to the ampulla of the posterior semicircular canal. The foramen endolymphaticum is a simple oval-shaped perforation in the dorsomedial wall of the prominentia cruris communis directly behind the prominentia utriculo-ampullaris posterior (inferior).

Due to the entire absence of the processus recessus, the presence of which is characteristic for Mammals only, the recessus scalae tympani is not included in the auditory capsule and consequently primitive conditions prevail in this region. The foramen perilymphaticum is large and situated in the extreme postero-ventral aspect of the cochlear capsule. It opens directly to the exterior of the auditory capsule as in primitive Mammalia and is bound in front by the posterior edge of the floor of the cochlear capsule and behind by the free anterior edge of the floor of the pars canalicularis. From the above description it will be clear that a true fenestra rotunda dose not exist in Eremitalpa at this stage of development.

The fissura metotica is undivided and has the shape of a simple cleft bound medially by the planum basale; laterally by the ventro-medial edge of the pars canalicularis; anteriorly by the fusion of the basal plate and auditory capsule in the form of the posterior basicochlear commissure and posteriorly by the processus alaris of the exoccipital cartilage. It transmits amongst others the IXth, Xth and XIth cranial nerves as well as the ductus perilymphaticus and the upper termination of the internal jugular vein.

The fenestra ovalis is a much elongated rectangular opening in the lateral wall of the vestibular segment of the pars cochlearis. It lodges the foot of the stapes and faces the sulcus facialis opposite the root of the tympano-hyale.

b. *The interior of the auditory capsule:* The membranous labyrinth is contained in a system of interconnecting spaces which, like the cartilaginous auditory capsule itself, can be divided into canicular and cochlear parts, the latter of which can again be subdivided into coclear and vestibular segments.

The cavum vestibulare, lying between the cavum cochleare and cavum canaliculare, is rather poorly delimited from these. It lodges the saccule, the canalis reuniens and the proximal portion of the ductus cochlearis. Antero-dorsally the cavum vestibulare communicates freely with the antero-ventral aspect of the most anterior part of the cavum canaliculare. This latter part of the cavum canaliculare lodges the greater part of the utricle and the ampullae of the anterior and lateral semicircular canals, being expanded as the recessus utriculo-ampullares anterior et lateralis for the reception of these. The posterior portion of the cavum canaliculare has a complete floor, the free anterior edge of which forms the posterior wall of the foramen perilymphaticum. In this region the cavum canaliculare expands into the recessus utriculo-ampullaris

VOL
28
194

posterior (inferior) which contains the posterior extremity of the utricle, the ampulla of the posterior semicircular canal and the posterior, non-ampullate, opening of the lateral semicircular canal. Immediately behind the recessus utriculo-ampullaris posterior the cavum canaliculare is continued as the sinus superior which lodges the crus commune of the anterior and posterior semicircular canals.

Owing to the very shallow fossa subarcuata superior externa the massa angularis is very thick.

The extreme anterior end only of the cavum vestibulare is delimited from the cavum cochleare by the basal end of the septum spirale; for the rest the cavum vestibulare communicates freely with the cavum cochleare ventromedially. Usually the medial end of the free anterior border of the floor of the cavum canaliculare is continued forwards as a ridge along the ventrolateral aspect of the dorso-medial wall of the pars cochlearis, thus partly separating the cavum vestibulare from the cavum cochleare but in Eremitalpa even this faint ridge is absent. Except for its extreme basal portion the septum spirale is still non-existent in Eremitalpa at this stage of development.

c. *Early development of the auditory capsule:* Up to the 21 mm stage the auditory capsule is entirely blastematous. At this stage it shows dense blastem concentrations—one in the pars cochlearis and another in the pars canalicularis. In the 24 and 25 mm embryos the otic capsule was found to be slightly chondrified except for the pars vestibularis which was still blastematous at this stage. From this it can be gathered that the otic capsule chondrifies from at least two centres: one in the pars cochlearis and another in the pars canalicularis. These centres are joined in the 27 mm embryo.

Regarding its connections to neighbouring parts of the chondrocranium the anterior basicochlear commissure is first defined in cartilage in the 27 mm embryo; the posterior basicochlear commissure is already present in the 25 mm stage but fusion with the lamina alaris of the exoccipital does not occur until in the 36 mm embryo.

The parietal plate arises from an autogenous centre being slightly chondrified in the 24 mm stage. Its attachment to the otic capsule at this stage is only in blastem and not until the 27 mm stage is cartilaginous continuity established between it and the otic capsule.

d. *Post optimal changes in the auditory capsule:* The tegmen tympani, which in the 28.5 mm embryo is only very poorly developed, increases in size markedly during the later embryonic stages, being a long and stout cartilaginous spur in the 45 mm embryo. Similarly the processus recessus, which in the 28.5 mm embryo is entirely absent, develops subsequently. In the 41 mm embryo and also in the 45 mm embryo it has the form of a short stout rod which is closely applied to the lateral edge of the planum basale. Posteriorly it ends blindly so that the recessus scala tympani still remains extra-capsular, the

fissura metotica undivided and the fenestra rotunda not defined. Also the septum spirale, which is hardly developed in the 28.5 mm embryo, becomes better defined in the later embryonic stages.

The processus opercularis has been mentioned as entirely absent in the 28.5 mm embryo. In the 41 mm stage a small, and in the 45 mm stage a much better developed processus opercularis is present, however. In the latter stage it forms a ridge on the upper aspect of the anterior part of the pars canalicularis lateral to the lateral jugular vein. It therefore helps to form a deep trough for the lateral jugular vein over the lateral aspect of the capsulo-parietal commissure. Actually the anterior upper edge of the opercular process fuses with the base of the parietal plate thus converting the deep trough for the lateral jugular vein into a canal anteriorly.

These relations in the Golden Mole seem to shed new light on the true nature of the opercular process. In the first instance the processus opercularis seems to represent a structure which develops in situ from the otic capsule, and which does not migrate into that position secondarily, as suggested by DE BEER (1929); furthermore its development seems to be associated with the protection of the lateral jugular vein. As its development in the mole proves, it may appear very late in ontogeny so that a processus opercularis may probably prove to be present in many Mammals in which it has been reported to be absent in relatively young embryonic stages.

Even in the oldest embryonic stage at my disposal (45 mm embryo), the auditory capsule is very poorly ossified; by far the greater part being still cartilaginous or only very slightly perichondrally ossified. However, three main ossification centres can be readily made out in the auditory capsule at this stage. Of these, two centres are observed for the first time in the 45 mm embryo, while only one centre can be made out in the 42 mm stage. The 42 mm embryo displays a rather limited zone of perichondral ossification in the pars canalicularis over the prominentia utriculo-ampullaris posterior (inferior). In the 45 mm stage this centre is still more or less isolated but is much more extensive (fig. 44) and affects the major parts of the prominentia utriculo-ampullaris posterior and the prominentia cruris communis. It extends almost as far back as the cupula posterior of the auditory capsule. In addition, the 45 mm embryo shows an autogenous ossification centre in the postero-inferior part of the pars cochlearis. This centre is rather limited at this stage. The antero-lateral part of the pars vestibularis of the auditory capsule also displays a fairly extensive ossification centre in the 45 mm embryo. Amongst others this centre involves the whole of the bridge of the foramen faciale secundarium and from it expands forwards in membrane bone fashion to help in the formation of the roof of the anterior part of the tympanic cavity.

No caudal or rostral entotympanics could be found in the embryonic stages

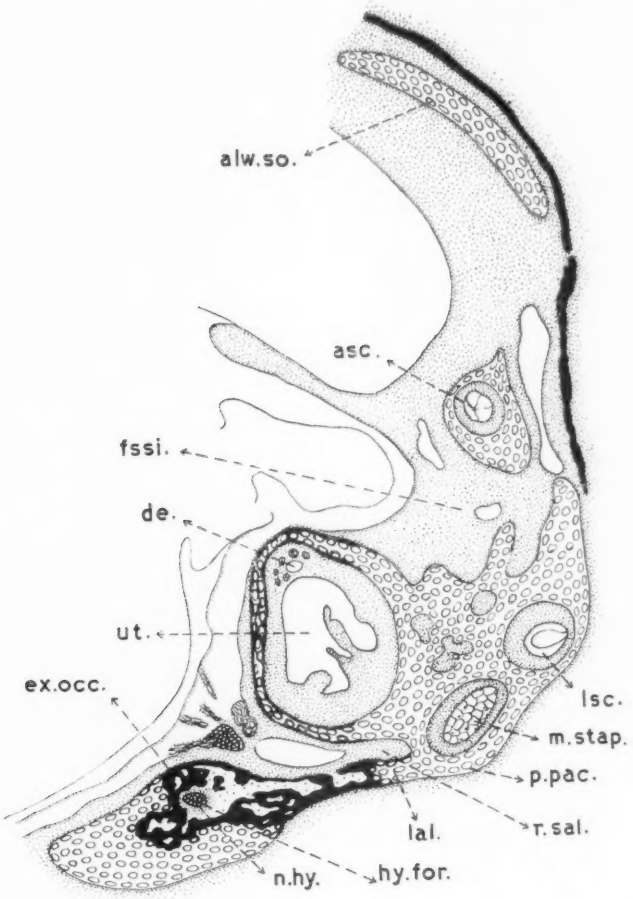

Fig. 44. Transverse section through the posterior part of the auditory capsule and ex-occipital region of a 45 mm embryo (× 15).

of the mole investigated; neither could any rostral or caudal petrosal tympanic plates be distinguished.

The cartilago tubae auditivae is well developed in the 42 mm and 45 mm stages. In the 41 mm embryo and also in the 45 mm embryo, the stapedial artery, as it passes lateral to the fenestra ovalis, is partly ensheathed in cartilage. This cartilaginous sheath has for the greater part the form of a trough but in parts it is tube-like. It pierces the stapedial fenestra together with the artery and attaches in front to the wall of he pars vestibularis, anterior to the fenestra ovalis. Posteriorly it attaches to the otic capsule postero-ventral to the fenestra ovalis. Cooper (1928) maintains that this cartilage becomes ossified in later development.

Another cartilage bar lies on the medial side of the internal carotid artery as it passes lateral to the fenestra ovalis. The connections of this bar are similar to those just described for the cartilaginous sheath of the stapedial artery.

3. The Ala Temporalis (figs. 38 and 41) in Eremitalpa is not very extensive, but, rather than being plate-like, it has the shape of a solid cartilaginous rod. It is joined to the antero-lateral edge of the lamina hypophyseos by means of the processus alaris. It is directed forwards, laterally and upwards; its posterior or basal portion being almost horizontal in position while its most anterior portion (processus antero-lateralis) is strongly inclined dorsally forming an angle of nearly 45° with the horizontal plane. The antero-lateral process extends forwards as far as the ala orbitalis, but is not pierced by a foramen and does not even show an incisura ovalis for the mandibular nerve; this nerve passes downwards postero-lateral to the ala temporalis. The pterygoid process (anterior process of FAWCETT) is short and directed antero-medially. It is not directly related to the pterygoid cartilage but lies close to the poorly developed pterygoid bone which, however, does not invade it at this stage of development. No foramen ali-sphenoidale for the infra-orbital artery or a foramen rotundum for the maxillary nerve is present. The infra-orbital artery remains ventral to the ala temporalis.

a. *Early development of the ala temporalis:* The ala temporalis in the 21 mm embryo is represented by an autogenous blastem rudiment which is in very slight continuity with the anterior end of the "polar element" of the lamina hypophyseos. In the 24 mm embryo it is slightly chondrified and the processus alaris, binding it to the lamina hypophyseos, is still procartilaginous so that the ala temporalis in the Golden Mole, as in the majority of Mammals, chondrifies from an autogenous centre. Cartilaginous continuity between ala temporalis and central stem is established in the 25 mm stage. As in Elephantulus (Author), the pterygoid process of the ala temporalis develops from an autogenous centre. In the 27 mm embryo it is well chondrified and in close contact with the blastem rudiment of the pterygoid cartilage, but its connections with the ala temporalis at this stage are only blastematous.

b. *Post optimal changes in the ala temporalis:* The ala temporalis ossifies to form the alisphenoid. The entire alisphenoid, however, is not preformed in cartilage but as in the orbitosphenoid and "tabular" (see later), the cartilage-bone expands in membrane-bone fashion to attain its adult compass. The first trace of an alisphenoid ossification was found in the 41 mm stage in the extreme anterior outer border of the ala temporalis. In the 45 mm embryo, almost the entire ala temporalis is ossified, leaving only a small nodule of cartilage in its anterior end and another more extensive nodule in its postero-medial end where it attaches to the central stem (fig. 45).

A foramen rotundum for the maxillary nerve is almost completely isolated. The alisphenoid forms the anterior ventro-lateral wall of the large anterior

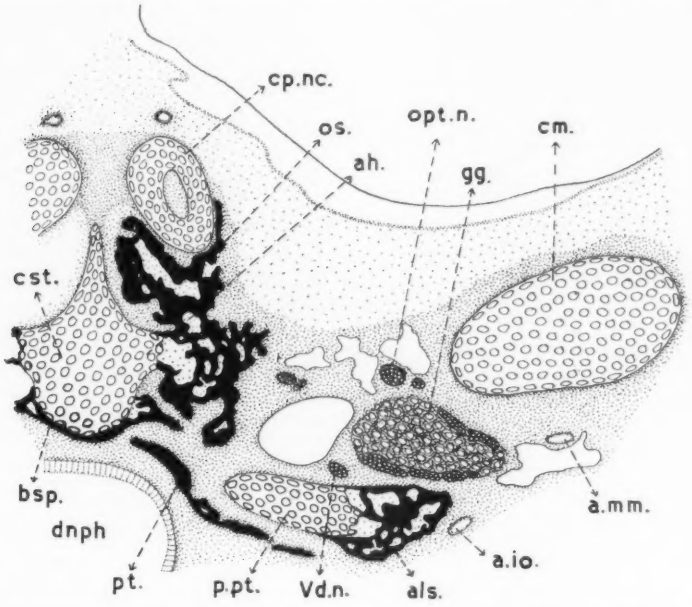

Fig. 45. Transverse section through the skull of a 45 mm embryo in the region of the ala hypochiasmata and orbitosphenoid (× 30).

superior part of the osseous bulla which lodges the large head of the malleus. In this position it is related to the squamosal, pterygoid, orbitosphenoid and basisphenoid. At no stage of its development is the ala temporalis invaded by the pterygoid, and in the latest embryonic stage investigated, the alisphenoid was found to be still separate from the pterygoid.

4. The Ala Orbitalis (figs. 37, 38) in Eremitalpa is a fairly extensive triangular cartilaginous plate which forms the ventral and ventro-lateral protection for the anterior part of the brain. Its anterior basal angle is connected to the frontal prominence of the pars intermedia of the nasal capsule by the wide sphenethmoidal commissure. Similarly its posterior basal angle is connected to the anterior edge of the parietal plate by the well-defined orbito-parietal commissure, thus completely isolating the extensive spheno-parietal fontanella, bound as follows: medially by the central stem, laterally by the orbito-parietal commissure, posteriorly by the auditory capsule and anteriorly by the ala orbitalis.

The apex of the ala orbitalis is directed medially and does not bifurcate to enclose the optic foramen but ends in a free pointed extremity dorsal to the ala hypochiasmata. The anterior border of the medial portion of the ala orbitalis rests on the dorsal postero-lateral aspect of the pars posterior of the nasal capsule.

The ala hypochiasmata has the shape of a large wing-like process directed antero-laterally. The optic nerve runs forwards and laterally dorsal to its posterior edge, but, since the ala hypochiasmata is in no direct cartilaginous continuity with the ala orbitalis, an optic foramen is absent: both pre- and post-optic roots being deficient. The absence of a post-optic root has thus far been reported in all Marsupials investigated (STADTMÜLLER 1936 and DE BEER 1937), as well as in Microtus (FAWCETT 1917), Miniopterus (FAWCETT 1919) and Galaeopithecus (HENCKEL 1929). The absence of a pre-optic root has only been reported in Dasyurus and Trichosurus (BROOM 1909) in which case, however, it is regarded as being incorporated in the cupula posterior of the nasal capsule.

Due to the intimate relations of the anterior edge of the ala orbitalis with the pars posterior of the nasal capsule the orbito-nasal fissure (ethmoidal fissure) is subdivided into a wide dorso-lateral division, which transmits the ophthalmic nerve and branches of the middle meningeal artery; and into a much smaller ventro-medial division: the foramen prechiasmaticum. This latter foramen is not completely isolated from the spheno-parietal fontanella due to the absence of the pre- and post optic roots of the ala orbitalis. For a review of the relations of the foramen prechiasmaticum in other Mammals the reader is referred to STADTMÜLLER (1936).

a. *Early development of the ala orbitalis:* The ala orbitalis is completely blastematous in the 21 mm embryo displaying blastem centres, one for the ala hypochiasmata, and another for the remaining part of the ala orbitalis. In the 24 mm embryo the ala hypochiasmata is still procartilaginous; in the 25 mm stage it is slightly chondrified but still separate from the central stem. Although well chondrified, the ala hypochiasmata does not fuse with the central stem until after the 27 mm stage. The rest of the ala orbitalis is slightly chondrified in the 24 mm embryo, its connections with the nasal capsule and parietal plate being still procartilaginous. Both the sphenethmoidal and orbito-parietal commissures are slightly chondrified in the 25 mm embryo.

b. *Post optimal changes in the ala orbitalis* (figs. 45 and 47): At no stage of its development does the ala hypochiasmata acquire any direct connections with the rest of the ala orbitalis since neither the pre- nor the post-optic roots of the ala orbitalis develop.

The ala hypochiasmata ossifies to form the orbitosphenoid. This orbito-sphenoid ossification was first observed in the 36 mm stage, at which stage it affects merely the anterior end of the ala hypochiasmata. In the 41 mm embryo the ala hypochiasmata is almost completely ossified and this ossification expands in membrane bone fashion forming a pneumatic, cup-shaped investment for the ventral, lateral and posterior aspects of the cupula posterior of the nasal capsule. There can be little doubt that it is this orbitosphenoid

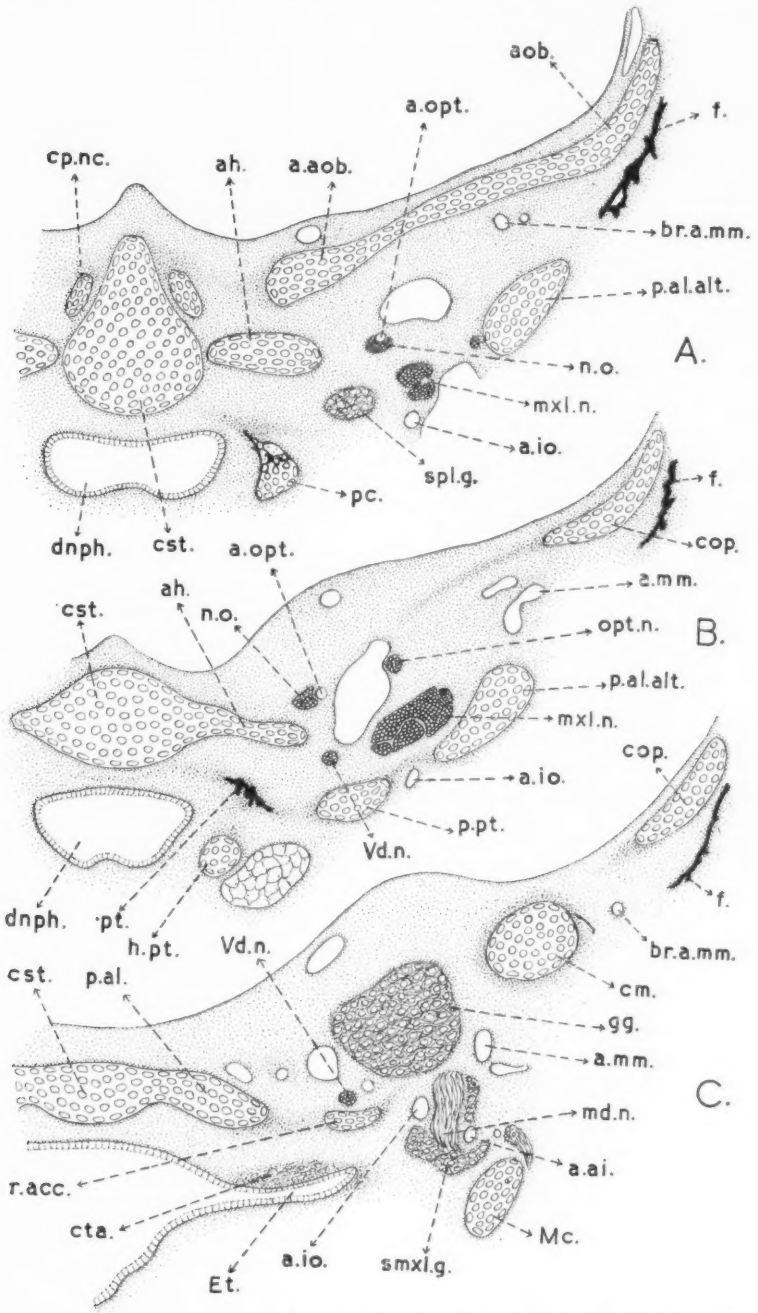

Fig. 46 A—C. Consecutive transverse sections through the sphenoidal region of the skull of a 28.5 mm embryo (× 45).

ossification which has been described as the problematic element "x" by BROOM (1916) for Chrysochloris.

The ala hypochiasmata is clearly indicated in BROOM's reconstruction (p. 455), but he did not appreciate that it was actually a part of the ala orbitalis, which, at this stage was already in an advanced stage of resorption. Had he done so, the significance of the element "x" would have become apparent, because this element would undoubtedly have been intimately connected to the ala hypochiasmata in the specimen he examined.

In the 45 mm embryo of Eremitalpa the orbitosphenoid is a fairly extensive antero-laterally directed osseous wing which bears a conspicuous ventral crest and still lacks an optic foramen.

COOPER (1928) maintains that a separate optic foramen does develop in the orbitosphenoid of the Golden Moles but that it is only visible from the inside of the skull.

The orbitosphenoid is related to the palatine, vomer, pterygoid, alisphenoid and basisphenoid. The latter relation is rather peculiar and is made possible by the extension of the basisphenoid ossification into the presphenoidal region of the central stem, thus becoming interposed between the medial ends of the two orbitosphenoids.

Apart from the ala hypochiasmata the rest of the ala orbitalis does not in any way contribute to the formation of the orbitosphenoid, but is completely resorbed in later development. In the 45 mm embryo the greater part of the ala orbitalis is very thin and already in an advanced stage of resorption, especially in its medial end; the sphenethmoidal commissure and antero-lateral part of the ala orbitalis being the best preserved. The orbito-parietal commissure is also completely resorbed at this stage except for a small rudimentary spur on the posterior end of the ala orbitalis.

5. The Nasal Capsule (figs. 37, 38 and 40): In contrast to the majority of Insectivores the nasal capsule of the Golden Mole is short, wide and strongly built. This is to be expected if one bears in mind the burrowing habits of the animal. Almost half of the nasal capsule is subcerebral in position, the remaining precerebral part inclining steeply forwards and downwards.

For descriptive purposes the nasal capsule can be divided into a pars posterior, a pars intermedia and a pars anterior, the boundaries of which will be described in due course.

Exterior of the Nasal Capsule:—Tectum nasi. The roof of the pars intermedia and pars posterior of the nasal capsule is subcerebral in position, slanting backwards and downwards at an angle of about 30°. It is most incomplete at this stage since the lamina cribrosa is very poorly developed. It consists mainly of the crista intercribrosa which represents the free upper edge of the

VOL
28
194

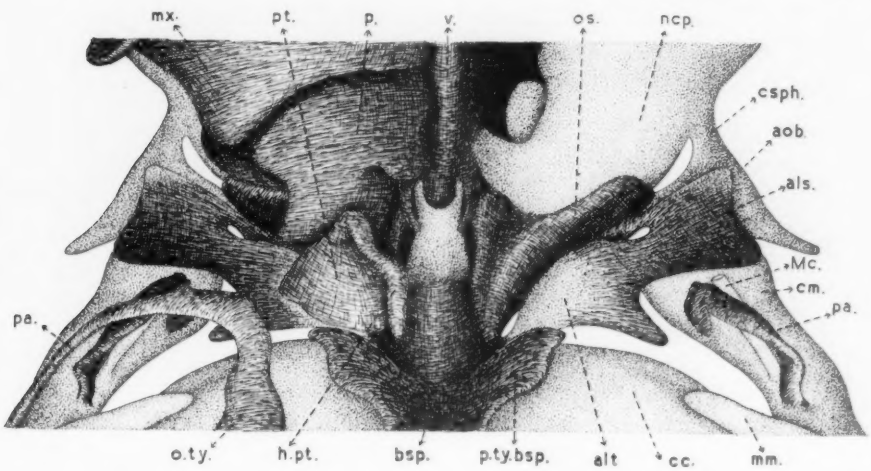

Fig. 47. Ventral view reconstruction of the sphenoidal region of the skull of a 45 mm embryo. Most of the membrane bones on the left side have been cut out of the reconstruction in order to show the sphenoids clearly (× 18).

posterior root of the first primary ethmoturbinal and which delimits a spacious antero-lateral fenestra from an even larger postero-medial fenestra. The tectum nasi posterius is complete and medially it is fused with the septum nasi; it is more steeply inclined backward than the rest of the lamina cribrosa. The upper edge of the septum nasi projects slightly between the two incomplete laminae cribrosae, thus constituting a fairly well-defined crista galli.

The precerebral portion of the tectum nasi slopes steeply downwards at an angle of about 45°. Medially the tectum is continuously blended with the upper edge of the septum nasi which lies in the floor of a well-defined sulcus dorsalis nasi. This sulcus, however, does not lead into a cavum internasale anteriorly, since the cupulae anteriores of the nasal capsule are not developed. Laterally the tectum nasi is fused with the upper edge of the paries nasi. A foramen epiphaniale is present on one side only—in an older stage it was found to be bilaterally represented.

The paries nasi is complete except for one deficiency, the fenestra superior nasi, near the tip of the snout. The pars posterior is small and poorly developed. It is demarcated from the pars intermedia by the poorly defined postero-lateral sulcus which runs downwards and slightly backwards and corresponds to the attachment of the middle and anterior roots of the first primary ethmoturbinal. On its outer surface it does not display any secondary sulci caused by the internal attachment of the second and third primary ethmoturbinals. Ventrally it is continued into the lamina transversalis posterior, dorsally into the tectum nasi posterius and posteriorly into the cupula posterior of the nasal capsule.

The pars intermedia projects far laterally due to the deep recesses which it lodges. Anteriorly it is delimited from the pars anterior by the antero-lateral sulcus corresponding to the internal attachment of the crista semicircularis. The attachment of the superior root of the first primary ethmoturbinal causes a deep sulcus on the lateral aspect of the pars intermedia. This sulcus delimits the prominentia superior (frontalis), which is postero-dorsal in position, from the prominentia anterior and the prominentia inferior (maxillaris). The sphenethmoidal commissure arises from the posterior dorso-lateral aspect of the prominentia superior.

The pars anterior in the Golden Mole is short and poorly developed, this part having undergone the greatest modification during the shortening of the snout. The free ventral edge of the paries nasi in the posterior two thirds of this region is bent medialwards and is slightly thickened to form the maxillo-turbinal; no lamina infraconchalis is present.

The posterior half of the pars anterior displays a deep sulcus postero-dorsally which corresponds to the attachment of the nasoturbinal. Below this sulcus lies the prominentia supraconchalis which projects backwards for some distance ventral to the prominentia anterior. The nasolacrimal canal runs obliquely upwards and backwards over the prominentia supraconchalis but is not lodged in a definite sulcus. In the anterior devision of the pars anterior (fig. 48) the ventral edge of the paries nasi is fused with the lateral edge of the lamina transversalis anterior for a short distance, thus resulting in the formation of a complete zona annularis. In this region the nasolacrimal canal is lodged in a deep sulcus along the ventro-lateral aspect of the zona annularis, this sulcus corresponding to the line of fusion between paris nasi and lamina transversalis anterior. The zona annularis is very narrow and anterior to it the nasolacrimal duct enters the cavum nasi through the posterior end of the fenestra naris, no separate foramen pretransversale being isolated for its transmission. Supero-lateral to the fenestra naris is situated a narrow elongated fenestra superior nasi (foramen dorsale of FAWCETT and fenestra lateralis of STURM). This fenestra is separated from the fenestra naris by a strip of paries nasi, which, at this stage, is not yet in cartilaginous continuity with the tectum nasi, anterior to the fenestra superior nasi; only a dense band of mesenchyme delimits the fenestra superior nasi from the fenestra naris anteriorly. The fenestra superior nasi faces downwards and laterally rather than upwards. At this stage of development no processus alaris superior, processus alaris inferior or processus cupularis is present. The fenestra naris is an extensive opening facing forwards and downwards.

The solum nasi (fig. 38). The floor of the posterior quarter of the nasal capsule is formed by the lamina transversalis posterior and the posterior paraseptal cartilage which springs from the antero-medial aspect of the lamina

VOL.
28
194

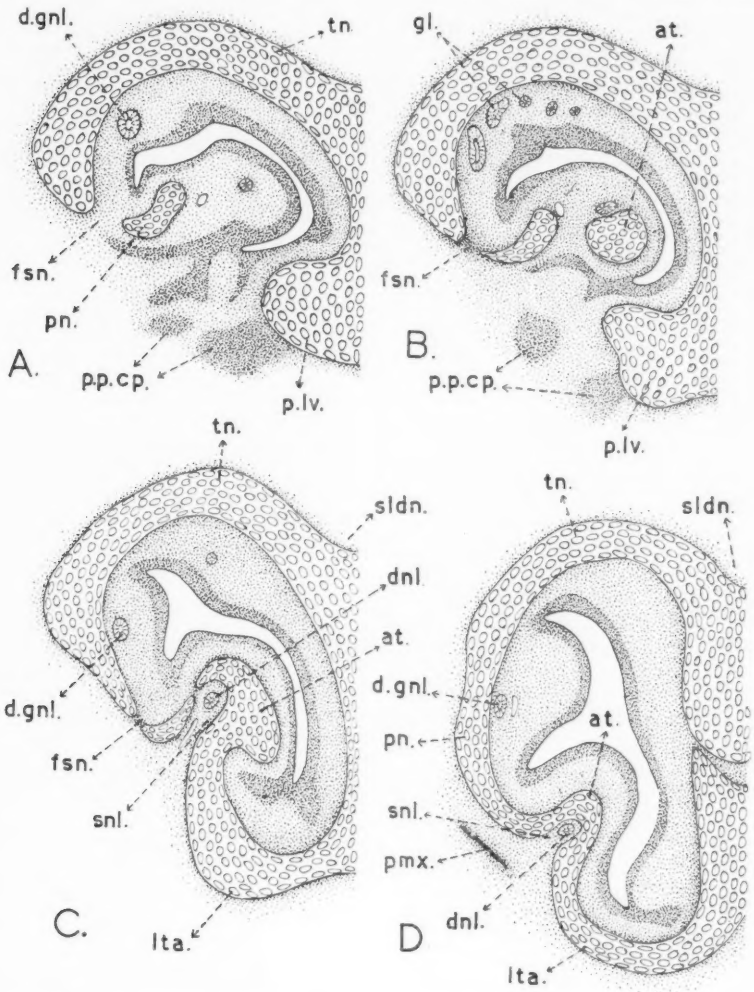

Fig. 48 A—D. Consecutive transverse sections through the tip of the snout of a 28.5 mm embryo (× 50).

transversalis posterior. Both the posterior paraseptal cartilage and the lamina transversalis posterior are separated from the nasal septum by a narrow fissure. The posterior paraseptal cartilage projects forwards to end blindly in the extensive fenestra basalis. Its anterior tip is separated from the posterior end of the anterior paraseptal cartilage by a wide gap. At this stage of development the posterior paraseptal cartilage is not as yet invaded by the vomer. A peculiarity of unknown significance is the presence of a flange of thin cartilage which surmounts the posterior paraseptal cartilage and is closely applied to the lateral aspect of the nasal septum (figs. 50, 53 A).

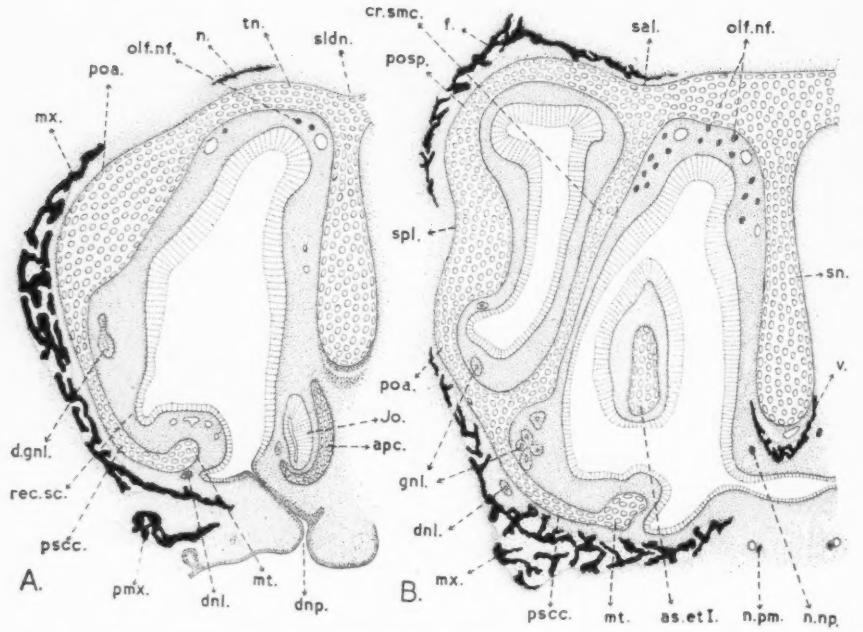

Fig. 49 A—B. Consecutive transverse sections through the nasal capsule of a 28.5 mm embryo (× 60).

The anterior paraseptal cartilage contributes to the formation of the floor of the middle portion of the nasal capsule, which, for the rest, is rather incomplete resulting in the formation of the extensive fenestra basalis. The anterior paraseptal cartilage itself is poorly developed. It consists for the greater part of a fairly wide vertically placed lamella which is separated from the nasal septum by a narrow septo-paraseptal fissure. Anteriorly the lamella fuses with the posterior border of the ascending medial wall of the lamina transversalis anterior. Only the extreme posterior portion of the ventral border of the vertical lamella is slightly recurved laterally, there being no trace of either an "outer bar" (BROOM), or a "lamina horizontalis" (STURM). The organ of Jacobson itself projects further back than does the vertical lamella of the anterior paraseptal cartilage. Both a cartilago ductus nasopalatini and a cartilago palatina are absent.

The lamina transversalis anterior forms the greater part of the floor of the nasal capsule in front of the fenestra basalis. Laterally it is fused with the ventral border of the paries nasi and medially the two laminae transversales anteriores fuse with the lower border of the nasal septum which, in this region, lies at a much lower level than it does between the two anterior paraseptal cartilages; the change, being abrupt, results in the formation of a little blind

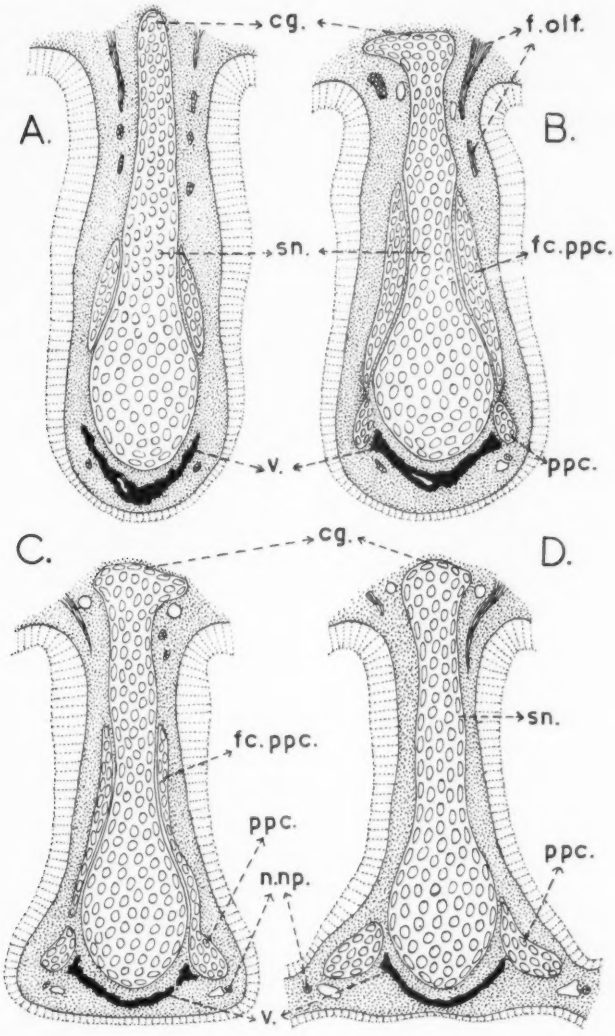

Fig. 50 A—D. Consecutive transverse sections through the nasal septum of a 28.5 mm embryo, in the region of the posterior paraseptal cartilages (× 70).

fossa in the nasal septum between the anterior extremities of the two anterior paraseptal cartilages. The sulcus ventralis nasi is shallow. Anteriorly the lamina transversalis anterior leads into the well-developed processus lateralis ventralis which tapers anteriorly and forms the ventral delimitation of the fenestra naris.

Interior of the Nasal Capsule (fig. 51): As in the majority of Mammals with a pronounced subcerebral lamina cribrosa the turbinal cartilages in the pars posterior and pars intermedia of the nasal capsule are almost vertically

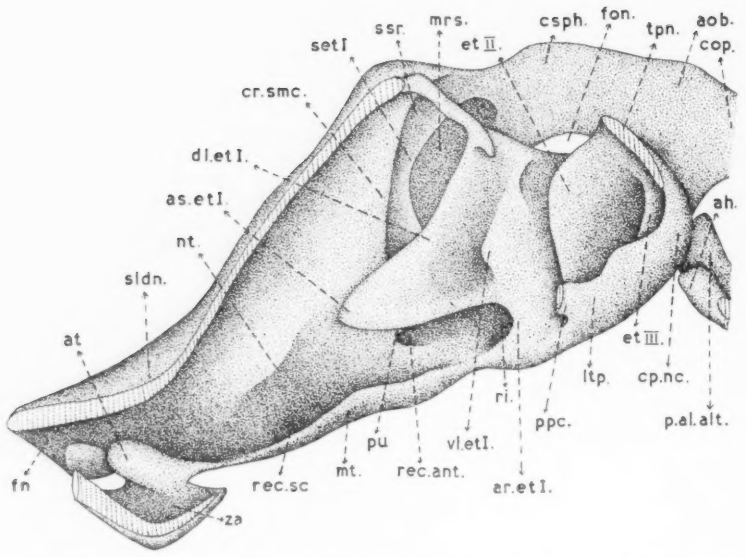

Fig. 51. Medial view reconstruction of the nasal capsule of a 28.5 mm embryo—the nasal septum has been cut out (× 30).

placed; these turbinals being usually arranged more or less at right angles to the lamina cribrosa. The turbinal cartilages divide the cavum nasi in this region into a series of recesses, which, like the turbinals themselves, are vertically placed.

The attachment of the first primary ethmoturbinal forms the anterior boundary of the pars posterior. This large and typically bilaminate turbinal arises from the tectum and paries nasi by four roots: the posterior root arises from the ventral aspect of the lamina chribrosa; the middle and anterior roots arise from the paries nasi, causing the sulcus postero-lateralis on its outer surface; the superior root arises from the medial aspect of the paries nasi in the pars intermedia and will be discussed later. The large upper or anterior lamella of the first primary ethmoturbinal projects very far forwards into the nasal cavity as a blindly ending spur, while the smaller lower or posterior lamella is relatively poorly developed at this stage. Apart from the first primary ethmoturbinal the pars posterior still lodges the second and third primary ethmoturbinals. Both these turbinals are, at this stage, of a simple unilamellar composition and in the intervening nasal recesses no trace of any secondary ethmoturbinals can be found.

The attachment of the crista semicircularis delimits the pars intermedia antero-dorsally, anteriorly and antero-ventrally. Externally it results in the formation of the sulcus antero-lateralis. The crista semicircularis is strongly developed and although its attachment describes an irregular semicircle with the

VOL
28
194

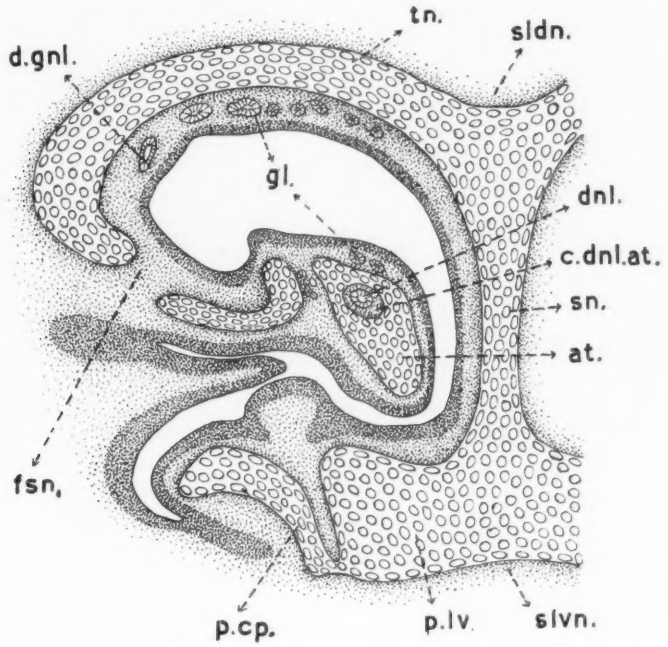

Fig. 52. Transverse section through the nasal capsule of a 45 mm embryo, taken near the tip of the snout (× 60).

convexity facing forwards its free edge, facing backwards, forms an almost vertical line, with the result that the bulk of the recessus anterior is hidden from view by the crista.

Postero-ventrally the crista semicircularis ends in a short processus uncinatus. Below and behind this process the crista semicircularis merges into the paries nasi and does not extend to its free ventral edge; consequently the recessus supraconchalis passes insensibly into the recessus inferior (maxillaris) behind. The attachment of the superior root of the first primary ethmoturbinal partly delimits the recessus inferior et anterior from the recessus superior (frontalis). The recessus superior, although deepest and therefore resulting in the most pronounced prominence externally, is not extensive. At its base, this recess lodges the first and second secondary ethmoturbinals; both these turbinals extend from the superior root of the first primary ethmoturbinal antero-ventrally to the lamina cribrosa postero-dorsally and are poorly developed at this stage. The presence of these two secondary turbinals in the recessus superior results in its subdivision into three secondary recesses, viz. a superior, a middle and an inferior secondary recess. Of these, only the superior secondary recess lying between the crista semicircularis and the first secondary ethmoturbinal, communicates freely with the recessus anterior. The recessus anterior is well developed and results in the conspicuous prominentia anterior

externally; ventrally it communicates freely with the recessus inferior (maxillaris) which is also well developed and projecting far backwards. The glandula nasalis lateralis in Eremitalpa is poorly developed, but some of its lobules penetrate into the subepithelial connective tissue which lines the recessus anterior et inferior.

The nasoturbinal is ill-defined and is restricted to the posterior half of the pars anterior. The maxilloturbinal is much better developed and, due to the absence of an incisura maxillo-atrioturbinalis, it is continued anteriorly into the atrioturbinal. The recessus supraconchalis, lying between the naso- and maxilloturbinals, is well-defined but lodges only the duct and a few lobules of the poorly developed glandula nasalis lateris. The atrioturbinal is strongly developed, being formed as the internal counterpart to the sulcus for the nasolacrimal duct in the region of the zona annularis.

The septum nasi (fig. 53 A) has the shape of a large triangle the base of which is formed by the free ventral edge of the nasal septum. This baseline is thickened and is not quite straight but describes a uniform curve the concavity of which is directed downwards. The apex, thus also the greatest dorso-ventral depth of the nasal septum, lies at the level of the anterior medial ends of the laminae cribrosae.

The postero-superior border of the nasal septum lies between the two cribriform plates. This border, like the ventral edge, is not quite straight, being slightly convex dorsally. This convexity projects above the plane of the cribriform plates as the crista galli. The antero-superior border is continuously blended with the medial edge of the tectum nasi, and at the junction of the anterior third and posterior two thirds of the pars anterior it displays a marked dorsally-facing concavity. No dificiencies are encounterad in the nasal septum at this stage of development.

a. *Early development of the Nasal Capsule:* The nasal capsule is entirely blastematous in the 21 mm embryo. The nasal septum, at this stage, is blastematously discontinuous with the rest of the nasal capsule, but the whole of the pars trabecularis of the central stem, including the part behind the nasal capsule, forms one continuous blastematous rod. The paries and tectum nasi are also well represented in blastem at this stage. They form one continuous blastem sheet for the pars anterior and pars intermedia, but the pars posterior displays a separate cell concentration. In the blastematous nasal capsule, therefore, the parieto-tectal and paranasal centres are already fused in the 21 mm embryo, while the antorbital centre (TERRY) still retains its separate identity. The anterior paraseptal in the 21 mm embryo displays an autogenous blastem centre.

In the 24 mm stage the greater part of the nasal capsule is defined in procartilage. The nasal septum is slightly chondrified in its posterior end; its

greater part, however, is procartilaginous and its extreme anterior tip is still blastematous. The pars anterior and pars intermedia of the tectum and paries nasi form a continuous procartilaginous sheet which is in procartilaginous continuity with the upper edge of the nasal septum in the region of the zona annularis; for the rest their attachment to the nasal septum is in blastem. The most anterior part of the paries nasi and the lamina transversalis anterior are still completely blastematous at this stage. An autogenous procartilage centre can be distinguished in the lamina verticalis of the blastematous anterior paraseptal. The pars posterior in the 24 mm embryo is almost exclusively blastematous.

In the 25 mm embryo conditions are very much the same as in the 24 mm stage with the only exception that the procartilage zones show slight signs of chondrification.

In the 27 mm embryo the nasal capsule

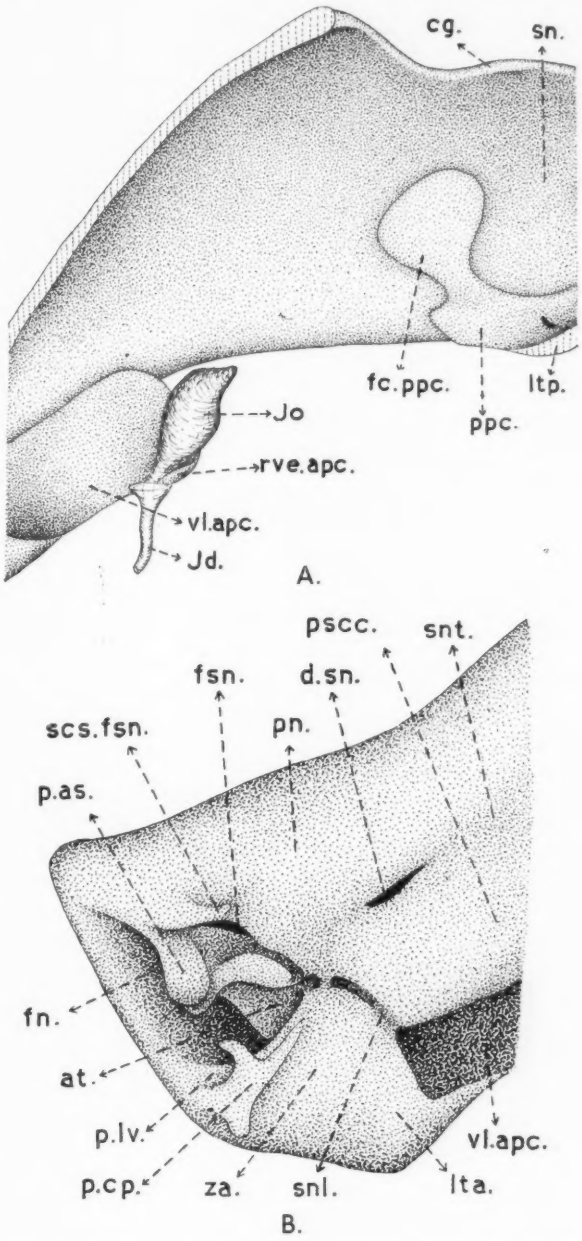

Fig. 53 A—B. — A. Lateral view reconstruction of part of the nasal septum, together with the anterior and posterior paraseptal cartilages and Jacobson's organ, in a 28.5 mm embryo (× 40). — B. Lateral view reconstruction of the tip of the snout in a 45 mm embryo (× 45).

is fairly well chondrified. The septum, tectum and paries nasi are in cartilaginous continuity with each other, except for the antorbital cartilage which is still slightly demarcated from the rast of the nasal capsule by procartilage.

The anterior paraseptal cartilage is continuous with the lamina transversalis anterior; its posterior end is still blastematous. Similarly the extreme anterior end of the nasal capsule is still partly blastematous. The lamina transversalis posterior and the posterior paraseptal cartilage develop in continuity with the paries nasi and do not arise from autogenous centres. They develop quite early, being already partly procartilaginous in the 24 mm embryo. The vertical flange of thin cartilage which surmounts the posterior paraseptal cartilage, displays a well-defined autogenous blastem centre in the 24 mm embryo; but it could not be determined, however, whether it chondrifies separately or in continuity with the posterior paraseptal cartilage.

b. *Post optimal changes in the Nasal Capsule* (figs. 52 and 53): A processus cupularis is entirely absent in the 28.5 mm embryo, but in the 45 mm embryo a well-developed processus cupularis of a rather complex nature is present. It arises relatively far back from the ventro-lateral aspect of the processus lateralis ventralis. This little process was observed for the first time as a slender cartilaginous rod in the 31 mm embryo. Similarly a processus alaris superior was reported to be absent in the 28.5 mm stage where the fenestra superior nasi was not even completely separated from the fenestra nasi by cartilage. In the oldest embryonic stage of the Golden Mole investigated, however, the fenestra superior nasi is completely delimited from the fenestra naris by a thin strand of paries nasi. This cartilaginous bar bears a small backwardly directed wing of cartilage on its antero-lateral aspect which could perhaps be homologized with the processus alaris superior of the other forms. Dorsal to the fenestra superior nasi the supero-lateral edge of the tectum nasi bears a short posteriorly directed cartilaginous spur in the older stages investigated.

The atrioturbinal in the 45 mm embryo is strongly developed; posteriorly it is directly continuous with the maxilloturbinal and anteriorly it projects for quite a distance in front of the zona annularis as a free pointed extremity. Along its lateral surface the atrioturbinal displays a deep groove for the nasolacrimal duct. This duct pierces the anterior end of the atrioturbinal, passing through a small foramen to open into the nasal cavity. The anterior end of the atrioturbinal in the advanced stages of development, therefore, is delimited from the paries nasi and also from the processus lateralis ventralis below by deep incisures which communicate freely with the extensive fenestra naris.

The sulcus for the nasolacrimal duct in the region of the zona annularis increases in depth with advancing age and in the 45 mm embryo it is in part even converted into a canal by a secondary growth of cartilage over its outer surface (compare Suncus: Author).

VOL
28
194

The nasoturbinal, which in the 28.5 mm stage was found to be rather poorly developed, increases in size rapidly during later development. In the 45 mm embryo it extends forwards into the region of the zona annularis as a prominent ridge to a point immediately behind the fenestra superior nasi. The duct from the glandula nasalis lateralis lies just below it in this region. The attachment of the nasoturbinal to the paries nasi results in the formation of a well-defined sulcus laterally; this sulcus extends forwards, over the zona annularis and delimits the prominentia supraconchalis dorsally. It displays a slight elongated deficiency at its base just above the attachment of the root of the nasoturbinal and about at the level of the posterior border of the zona annularis.

The glandula nasalis lateralis, which is very poorly developed in the 28.5 mm embryo, is of enormous size in the 45 mm stage and lines the greater part of the recessus supraconchalis as well as the entire recessus inferior et anterior.

In the 31 mm embryo a third secondary ethmoturbinal already makes its appearance at the base of the deep recess between the first and second primary ethmoturbinals. At this stage the second primary ethmoturbinal also shows the first signs of becoming bilaminate; the small newly formed lamella lies lateral to the main lamella of the turbinal and even in the 45 mm stage remains relatively poorly developed.

The anterior paraseptal cartilage in the 45 mm embryo still has the shape of an extensive vertically placed lamella which does not extend as far back as the organ of Jacobson does. The ventral edge of the posterior end is however, a little stronger recurved laterally than is the case in the 28.5 mm embryo, but an "outer bar" remains completely deficient. It will be recalled, however, that BROOM (1915) described an "outer bar" as present in a newly born specimen of *Chrysochloris* (*Amblysomus*) *hottentotta*, and it is thus possible that this structure may still appear during later development in Eremitalpa.

A small and ill-defined cartilago ductus nasopalatini is present in the 45 mm embryo. It makes its first appearance at this stage and is irregularly C-shaped, enclosing the nasopalatine duct anteriorly, laterally and posteriorly. It has no direct communication with the anterior paraseptal cartilage.

A cartilago palatina is still absent in the 45 mm embryo. In the latest embryonic stage investigated very little resorption of cartilage has taken place in the nasal capsule. In the 45 mm embryo the greater part of the roof of the superior secondary recess of the recessus frontalis (superior) is deficient. Similarly the lateral wall of the middle secondary recess of the recessus frontalis displays a fairly extensive resorption deficiency in its anterior part. Both these deficiencies are completely roofed over by the frontal.

The posterior end of the maxilloturbinal, at this stage, is also separated from the lower edge of the paries nasi by a deep resorption incisure.

The ossification of the nasal capsule in the 45 mm embryo is rather limited. There is no trace of a medial mesethmoid ossification centre as yet, although the laminae cribrosae are fully developed at this stage. The main ossification centre of the lateral pleurethmoid first appears in the 41 mm embryo as a slightly perichondrally ossified area in the ventral border of the anteriorly directed spur of the first primary ethmoturbinal. In the 45 mm embryo this centre is still isolated but is much more extensive, involving the greater part of the anterior spur and ventral lamella of the first primary ethmoturbinal. In addition, the 45 mm embryo displays an autogenous ossification centre in the processus uncinatus of the crista semicircularis, while the maxilloturbinal also shows signs of slight perichondral ossification. The posterior paraseptal cartilage and the lamina transversalis posterior ossify from a separate centre, being already invaded by the vomer in the 31 mm embryo.

C. THE DORSAL STRUCTURES.

The only true part of the roof of the cranial cavity is the tectum posterius which delimits the foramen magnum postero-dorsally. The tectum posterius is a slender transverse cartilaginous rod which is composed of the fused supra-occipital cartilages. Laterally it fuses with the exoccipital, and expands anteriorly into a wide wing-like cartilaginous protection for the postero-lateral part of the brain.

This large antero-laterally directed wing of the supraoccipital is rather peculiar of the Golden Mole. Its extensive development is probably responsible for the poor development of the posterior part of the parietal plate and the deficiency of the occipito-parietal commissure.

1. Early development of the supraoccipital cartilages: The supraoccipital cartilage makes its first appearance as a slight chondrification in the 25 mm embryo. At this stage it is already in sligth continuity with the upper posterior end of the exoccipital cartilage. It bears a wide anteriorly directed flange of thin procartilage. The tectum posterius is not quite complete at this stage, the two supraoccipital cartilages being separated by a narrow strand of dense blastem. In the 27 mm embryo the supraoccipital is well chondrified, including the extensive anteriorly directed plate. The tectum posterius is also complete but the junction between the supra- and exoccipital cartilages is still clearly defined by a narrow strand of seemingly extremely compressed cartilage cells.

2. Post optimal changes in the supraoccipital cartilages: The supraoccipital ossification appears very soon after the completion of the tectum posterius in cartilage. In the 28.5 mm embryo it is already fairly extensive, although only perichondral in nature and involves almost the entire tectum posterius. It was not possible, therefore, to determine

VOL 28 194

whether or not it arises from two ossification centres. Up to the 36 mm stage no trace of an interparietal could be found. In the 41 and 45 mm stages, however, an extensive unpaired bony plate was found to roof the postero-dorsal part of the cavum cranii. This plate passes insensibly into the supraoccipital behind and postero-laterally it invades the upper edge of the anteriorly directed wing of the supraoccipital cartilage. Whether this plate represents an interparietal which is formed fairly late in ontogeny and which fuses with the supraoccipital again immediately after its formation could not be determined beyond any doubt.

The 31 mm embryo shows an autogenous ossification centre in the postero-ventral border of the anteriorly directed plate of the supraoccipital cartilage, directly dorsal to its junction with the exoccipital cartilage. This centre expands rapidly forwards and upwards by the ossification of the mentioned anterior plate of the supraoccipital. It also expands forwards in membrane bone fashion thus covering over the upper part of the occipito-capsular fissure and overlapping the pars canalicularis postero-dorsaly. In the 45 mm embryo this bony plate is already fairly extensive but at this stage it bears no direct relations with any of the neighbouring bony elements except for the parietal which meets it antero-dorsally; strands of supraoccipital cartilage still intervene between it and the supra- and exoccipital ossifications. In later development it fuses with the surrounding bony elements, i.e. with the parietal, squamosal, ex- and supraoccipitals and with the interparietal.

This bony element was first described as the tabular in Chrysochloris by BROOM (1916). He regarded it as homologous with the tabular found in the Theromorpha. Actually LECHE (1907) was the first person who described this element in Chrysochloris, referring to it as the pterotic.

This element was known to be present in Phoca even before it was discovered in Chrysochloris. Its preformation in cartilage, belonging to the supraoccipital, in the Golden Mole is undoubtedly of great importance since this element has in the past been regarded as being a true membrane bone.

IV. THE MEMBRANE BONES.

For a description of the membrane bones a 45 mm embryo i.e. the oldest embryonic stage at my disposal, has been selected.

A. THE PREMAXILLA

is well-developed with a large alveolar portion but a very short processus extranasalis. The palatine process is also well-defined and the posteriorly directed processus palatinus medialis (Processus prevomeralis) is strongly

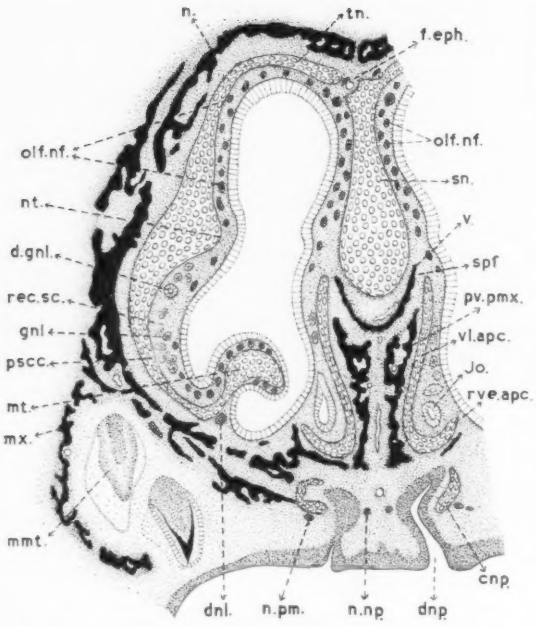

Fig. 54. Transverse section through the nasal capsule of a 45 mm embryo, in the region of the anterior paraseptal cartilages (× 40).

developed and markedly pneumatic in its anterior part. It is closely related to both the maxilla and vomer but does not fuse with either of these elements at this stage. It has the shape of a broad vertically placed lamella which covers the greater part of the medial surface of the anterior paraseptal cartilage (fig. 54). In the adult the two premaxillae fuse in the middle line and they also fuse completely with the maxillae and nasals.

The premaxilla makes its first appearance in the 24 mm embryo as a minute splint of bone which occupies the position of the future alveloar portion. In the 27 mm embryo the bone is fairly well developed but the processus prevomeralis is still absent. This process is present and fused with the rest of the premaxilla in the 28.5 mm stage, so that it was not possible to determine whether or not it arose from an autogenous centre.

B. THE MAXILLA

bears the usual large and flat frontal process which covers the greater part of the prominentia supraconchalis, prominentia inferior and prominentia anterior. At this stage it is related to the premaxilla, nasal, frontal and lacrimal. The alveolar portion is well-developed as also the medially extending palatine process which is separated from its fellow on the opposite side by a strand of secondary cartilage. The most anterior medial end of the palatine process of the maxilla is surmounted by a small vertically placed bony lamella which helps the processus prevomeralis of the premaxilla to form the medial support for the anterior paraseptal cartilage. On its postero-lateral surface the maxilla gives rise to a stout backwardly directed zygomatic process. This process actually arises by two roots: the upper root is the more slender and arises from the frontal process of the maxilla, the lower root is stronger and arises

VOL 28 194

from its alveolar portion. Between the two roots lies the infraorbital foramen for the transmissian of the infraorbital nerve.

The zygomatic process is very long and forms a complete zygomatic arch as in the Monotremes. Posteriorly the zygomatic process of the maxilla widens out into a fairly thin but wide vertically placed lamella which, at this stage, bears no close relation to the squamosal.

In its later development the maxilla becomes completely fused with the premaxilla, nasal, frontal, lacrimal, palatine and with its fellow on the opposite side; it does not, however, fuse with the squamosal but merely forms a syndesmosis with it.

The maxilla makes its first appearance in the 24 mm embryo. At this stage it displays two definite centres of ossification: one in the base of the frontal process i.e. just above the alveolar portion and another in the anterior end of the future zygomatic process. These two centres of the maxilla remain separate until after the 28.5 mm stage when they fuse The most anterior centre forms the entire maxilla except for the zygomatic process. The posterior centre expands backwards to form the entire zygomatic arch; its anterior end splits to enclose the infraorbital foramen below and behind. The lower limb fuses with the postero-lateral tip of the alveolar portion of the maxilla in the 31 mm embryo. The slender upper limb expands into a flat bony plate on the lateral aspect of the nasal capsule, and this plate, in the 31 mm embryo, becomes fused with the frontal process of the maxilla.

This development of the maxilla strongly suggests the presence of a well-defined jugal which becomes fused with the maxilla at a relatively early stage of development. Up till now the presence of a jugal in the Golden Mole has been denied by all investigators into the group (Broom 1916, Leche 1907, Gregory 1910, Cooper 1928 and others).

According to Gregory the zygomatic arch of the Chrysochloridae is entirely secondary. Being derived from an ancestral form that had already lost the primary arch the new arch in the Chrysochloridae, is formed by a secondary growth of the maxilla towards the squamosal. Cooper (1928) strongly supports this view of Gregory.

C. THE LACRIMAL BONE

at this stage is a small flat table of bone closely applied to the upper border of the prominentia inferior. It lies postero-dorsal to the infraorbital foramina, between the inferior border of the frontal above, and the maxilla below. It is not pierced by the nasolacrimal duct which runs medially between the lacrimal bone and the maxilla. During its later development the lacrimal bone fuses both with the frontal and with the maxilla, the lacrimal canal being retained between it and the maxilla.

The lacrimal develops very late and was observed for the first time in the 45 mm embryo.

D. THE JUGAL (ZYGOMATICUM OR MALARE)

is commonly regarded as absent in the Golden Mole but, as in Echidna, the zygomatic arch is still complete. In Ornithorhynchus, Manis and the Myrmacophaga the jugal has been reported as rudimentary. In all the Insectivores except Tupaiidae and Macrocelidae the jugal is absent or rudimentary, with a consequent poorly developed or deficient zygomatic arch.

The development of the zygomatic arch in the Golden Mole however, suggests the presence of a well-defined jugal which becomes fused with the maxilla in the 31 mm embryo (see development of maxilla).

E. THE PALATINE

is large and well-developed. The lamina horizontalis meets its fellow from the opposite side in the middle line, displaying nodules of secondary cartilage along this juncture. It forms the anterior boundary of the apertura nasalis interna.

The lamina verticalis forms a wide trough-shaped investment for the ventral surface of the lamina transversalis posterior. The medial wall of this trough forms the lateral wall of the ductus nasopharyngeus and meets the vomer above. Anteriorly the palatine is slightly overlapped by the palatine process of the maxilla and posteriorly by the pterygoid.

During later development the horizontal lamina of the palatine fuses with the maxilla and also with its fellow from the opposite side, but it does not fuse either with the vomer or with the pterygoid, forming merely intimate sutures with these elements.

The palatine was observed for the first time in the 28.5 mm embryo. At this stage it was already fairly well ossified so that the exact position of its ossification centre could not be determined.

F. THE VOMER

is an unpaired trough-shaped bone which invests the lower surface of the nasal septum from between the anterior paraseptal cartilages to a point between the cupulae posteriores of the nasal capsules. Its anterior end is related to the processus prevomerales of the premaxillae and also to the palatine processes of the maxillae; posteriorly it is related to the vertical laminae of the palatines and to the orbitosphenoids.

VOL. 28 194

The lateral walls of the trough-shaped vomer are much thicker than its floor, being even pneumatic in parts; they invade the posterior paraseptal cartilages but do not affect the anterior paraseptal cartilages. The bottom of the vomer is very thin, compact and in parts deficient, resulting in the formation of several large foramina.

Judging from its relations to the posterior paraseptal cartilage and lamina transversalis posterior one can surmise that in the adult the vomer will be inseparably fused with the ethmoid as is usually the case

The vomer makes its first appearance in the 27 mm embryo as a minute splint of bone ventral to the nasal septum. As a rule the vomer in Mammals arises ontogenetically from two centres which fuse soon after their formation. In the 28.5 mm embryo the vomer is already trough-shaped but it does not invade the posterior paraseptal cartilages as yet. In the 31 mm stage, however, the vomer has begun its invasion of the extreme anterior tips of the posterior paraseptal cartilages.

OL.
28
947

G. THE PTERYGOID

is well developed consisting for the greater part of a flat slightly concave plate which lies ventral to the posterior part of the palatine, the orbitosphenoid and part of the alisphenoid. It forms part of the lateral wall of the nasopharyngeal canal. The long hamulus projects downwards and backward from the anterior ventro-medial end of the pterygoid to help support the soft palate. At this stage of development the bone is not fused to any other bones in its vicinity and does not invade the ala temporalis.

In the 27 mm embryo only a dense cell concentration marks the position of the future pterygoid. This blastem rudiment is intimately related to the cartilaginous pterygoid process of the ala temporalis. In the 28.5 mm embryo the pterygoid cartilage is well defined and forms the bulk of the pterygoid at this stage. Only a small postero-laterally directed bony spur is present and this spur is in direct continuity with the pterygoid cartilage.

During its later development the pterygoid increases greatly in size, but in the oldest embryonic stage of the Golden Mole investigated (45 mm), it is still completely separate from the alisphenoid and from the other neighbouring bony elements.

H. THE NASAL

is a well-defined bony plate which roofs the anterior part of the nasal capsule. It presents nothing of particular interest, save that in later development it fuses with its fellow in the median plane and also with the neighbouring bony elements, i.e. with the frontal, maxilla and premaxilla.

The nasal was first observed in the 28.5 mm embryo where it was already fairly extensively ossified.

I. THE FRONTAL

is a bony plate of moderate size which, like the nasal, presents nothing of particular interest. At this stage of development it is still completely separate from all the neighbouring bony element being related to: nasal, maxilla, lacrimal, parietal, orbital process of palatine, orbitosphenoid and alisphenoid.

Along its dorso-lateral edge it is thick and strongly pneumatic displaying an extensive frontal sinus. No postorbital process can be distinguished on the frontal. During later development the frontal fuses with its fellow from the opposite side as well as with the parietal maxilla, lacrimal palatine and sphenoids.

The frontal ossification makes its first appearance in the 24 mm stage lying dorso-lateral to the prominentia superior of the nasal capsule and lateral to the base of the ala orbitalis.

VOL 28 194

J. THE PARIETAL

is a thin but very extensive bony plate which roofs the greater dorso-lateral part of the cavum cranii. It is related to the frontal, squamosal, tabular and interparietal, fusing with all these elements during the later stages of development.

It makes its first appearance in ontogeny as a thin bony plate lying dorso-lateral to the parietal plate in the 28.5 mm embryo.

K. THE SQUAMOSAL

is well developed but of a most peculiar shape. The glenoid cavity is ill-defined, being merely a small horizontal shelf for the reception of the articular process of the dentary. A processus postglenoideus is absent. Above the glenoid cavity the lateral surface of the squamosal displays a long vertical ridge with which the widened posterior edge of the long zygomatic process of the maxilla articulates. Behind this ridge the squamosal bears a long process directed backwards and downwards. This process, which lies lateral to the otic capsule, is related to the parietal and tabular and later in its development extends as far back as to reach the exoccipital (BROOM 1916).

The osseous bulla in the Golden Mole is well developed in the adult and consists of a medial postero-ventral portion and a large lateral antero-dorsal portion. This latter portion surrounds the enormously enlarged recessus epitympanicus of the middle ear which lodges the large head of the malleus. The

postero-ventrally directed process of the squamosal contributes to the formation of the posterior division of the osseous bulla.

In front of the glenoid cavity the squamosal expands in a forward and downward direction to meet the alisphenoid, thus contributing to the formation of the floor and lateral wall of the large anterior portion of the osseous bulla.

The squamosal ossifies from a single centre which makes its appearance in the 24 mm embryo as a minute splint of bone lateral to the posterior end of the head of the malleus.

L. THE TYMPANIC (ECTOTYMPANIC),

at this stage of development forms about seven-eighths of a circle with the deficiency directed upwards, sideways and backwards. Its relations to the prearticular and Meckel's cartilage are as usual. During later development the tympanic bone loses its C-shape and plays an important part in the formation of the osseous bulla.

It arises from a single centre which appears in the 28.5 mm embryo as a slightly bent, bony spur lying in front of the tympanic cavity.

M. THE PREARTICULAR (GONIAL)

is a well-defined bony plate which lies ventro-lateral and ventral to the posterior extremity of Meckel's cartilage (fig. 47). The anterior end of the prearticular is wide and forms a shallow trough investing the ventral surface of Meckel's cartilage in this region. The medial wall of the trough extends backwards as a free pointed spur which lies ventro-medial to Meckel's cartilage. This small spur occupies exactly the same position as the surangular described for Chrysochloris (Broom 1916) and (Cooper 1928), but it is not separate from the prearticular. The lateral wall of the trough extends backwards dorso-medial to the tympanic and ventro-lateral to Meckel's cartilage. Its posterior end invades the neck of the malleus ventro-lateral to the attachment of Meckel's cartilage.

The prearticular makes its first appearance in the 28.5 mm stage where it has the form of a very tiny bony spicule ventro-lateral to the extreme tip of Meckel's cartilage. Its posterior end does not commence its invasion of the neck of the malleus until after the 36 mm stage.

N. THE TABULAR AND INTERPARIETAL

have been discussed in connection with the supraoccipital.

VOL. 28 1947

V. SUMMARY.

The following points in the development of the chondrocranium and early osteocranium of *Eremitalpa granti* (BROOM) are noteworthy:

a. *The central stem.*

1. The central stem is acutely flexed in the region of the dorsum sellae.
2. No fenestra hypophyseos or posterior basicranial fenestra is retained at the optimal stage of chondrification.
3. The basicochlear fissure is present and undivided.
4. The anterior part of the basal plate is exceedingly compressed by the cochlear capsules.
5. The alicochlear commissures are deficient and not even preformed in blastem.
6. The dorsum sellae is well-defined and the fossa hypophyseos is deep.
7. No trace of the notochord is left at the stage of optimal chondrification of the planum basale.
8. The carotid foramina are very far laterally placed.
9. The fenestra hypophyseos is obliterated very early in ontogeny, and no separate "polar elements" can be distinguished in the development of the lamina hypophyseos.
10. Before being absorbed, the anterior part of the notochord is embedded in the basal plate but its posterior part lies superficial (dorsal) to it.
11. The adult basicranial axis consists of three unpaired elements only. The basisphenoid extends relatively far forward and the orbitosphenoids do not enter into the formation of the axis. (The most anterior ossification centre could not be determined from the material investigated).
12. The basisphenoid bears a pair of conspicuous tympanic wings.

b. *Exoccipital cartilages.*

1. A single pair of hypoglossal foramina is present.
2. The lamina alaris is merely closely applied to, but not fused with, the pars canalicularis of the otic capsule at its optimal stage of development.
3. The superior and inferior occipito-capsular fissures are confluent.
4. The processus paracondyloideus is inconspicuous.
5. A separate chondrification centre for the exoccipital could not be distinguished.
6. The lamina alaris does not fuse with the otic capsule until very late in development.
7. The exoccipital ossifies from a single centre.
8. The paracondyloid process ossifies in continuity with the exoccipital.

VOL
28
194

c. *Auditory capusule.*

1. The antero-ventral convergence of the two auditory capsules is pronounced.
2. A posterior occipito-capsular commissure is absent.
3. The parietal plate is ill-defined.
4. The occipito-parietal commissure is deficient.
5. A processus opercularis (FISCHER) is absent at the optimal stage of chondrification of the auditory capsule, but appears in later development.
6. The tegmen tympani is short and blunt.
7. The primary suprafacial (medial prefacial) commissure is well-defined, but the secondary suprafacial (lateral prefacial) commissure is absent.
8. The fossa subarcuata superior interna is well-developed.
9. The fossa subarcuata inferior interna is ill-defined.
10. The pars cochlearis displays a well-defined sulcus for the internal carotid artery and deep petrosal nerve, but no sulcus septalis.
11. A separate foramen for the lower nerve to the saccule and a separate foramen singulare are absent.
12. The foramen endolymphaticum is a simple oval-shaped perforation in the dorso-medial wall of the prominentia cruris communis.
13. The processus recessus and associated structures display rather primitive relations.
14. The fissura metotica is undivided.
15. The fenestra ovalis is extensive.
16. The auditory capsule chondrifies from two main centres.
17. The parietal plate chondrifies from an autogenous centre.
18. The tegmen tympani increases markedy in size during later development.
19. The auditory capsule ossifies from three main centres.
20. No caudal or rostral entotympanics or caudal and rostral petrosal plates could be made out.
21. The cartilago tubae auditivae is well-defined in later development.

d. *Ala temporalis.*

1. The ala temporalis is slender and rod-like and strongly inclined dorsally.
2. It does not display any foramina for vessels or nerves.
3. It is not connected with the cochlear capsule, due to the deficient alicochlear commissure.
4. A pterygoid process is present but small.
5. The ala temporalis chondrifies from an autogenous centre.
6. The pterygoid process of the ala temporalis likewise chondrifies from a separate centre.
7. The alisphenoid ossifies from a single centre and the pterygoid bone does not invade the ala temporalis at any stage of its development.
8. A processus tympanicus alisphenoidei is present.

VOL. 28 1947

e. *Ala orbitalis.*

1. Both the sphenethmoidal and the orbito-parietal commissures are well-defined.
2. The ala hypochiasmata is extensive and fused with the pars trabecularis.
3. An optic foramen is not defined due to the absence of both pre- and post-optic roots of the ala orbitalis.
4. The ala hypochiasmata chondrifies from an autogenous centre which retains its separate identity for long.
5. The rest of the ala orbitalis also displays a separate chondrification centre.
6. Pre- and post-optic roots of the ala orbitalis never develop.
7. The entire orbitosphenoid ossification eminates from the ala hypochiasmata and expands in membrane bone fashion.

f. *Nasal capsule.*

1. The nasal capsule is short wide and strongly built.
2. Almost half the nasal capsule is subcerebral in position.
3. The tectum nasi posterius is complete and is more steeply inclined backwards than the lamina cribrosa.
4. The crista galli is fairly well defined.
5. A cavum internasale is not defined due to the absence of the cupulae anteriores of the nasal capsule.
6. The foramen epiphaniale is present.
7. No lamina infraconchalis is defined.
8. A complete zona annularis is present.
9. The nasolacrimal duct is lodged in a deep sulcus and enters the cavum nasi through the posterior end of the fenestra narina—a foramen pretransversale being absent.
10. A fenestra superior nasi is present.
11. The fenestra naris is extensive and faces forwards and downwards.
12. The small nasal cartilages round the fenestra naris become differentiated fairly late in ontogeny.
13. A processus cupularis, of complex nature, develops.
14. A processus alaris superior also makes its appearance in later development.
15. The lamina transversalis posterior is well-defined.
16. The posterior paraseptal cartilage is present and is surmounted by a flange of thin cartilage, closely applied to the lateral aspect of the nasal septum.
17. The anterior paraseptal cartilage is of a very primitive composition, and an "outer bar" was found to be absent.
18. The turbinal cartilages in the pars posterior and pars intermedia of the nasal capsule are almost vertically placed.
19. The crista semicircularis bears a short processus uncinatus.

VOL
28
194

20. An incisura maxillo-atrioturbinalis is absent and consequently the maxilloturbinalis is continued anteriorly into the atrioturbinal.
21. The nasal septum displays no deficiencies.
22. In late embryonic stages the nasolacrimal duct is found to pierce the anterior tip of the atrioturbinal before entering the cavum nasi.
23. In older embryonic stages the deep sulcus for the nasolacrimal duct in the region of the zona annularis is partly transformed into a canal.
24. The glandula nasalis lateralis is of enormous size in the oldest embryonic stages investigated.
25. In the later embryonic stages investigated three secondary ethmoturbinals were found to be present and the second primary ethmoturbinal was found to be bilaminate in addition to the first.
26. A small cartilago ductus nasopatini is present in late ontogeny but it remains separate from the anterior paraseptal cartilage.
27. The anterior paraseptal cartilage chondrifies from an autogenous centre.
28. A well-defined antorbital chondrification centre could be distinguished in the nasal capsule.
29. The main pleurethmoidal ossification centre makes its appearance in the anteriorly directed spur of the first primary ethmoturbinal.
30. The maxilloturbinal and the processus uncinatus display autogenous ossification centres.
31. The lamina transversalis posterior and posterior paraseptal cartilage are invaded by the vomer relatively early in development

OL.
28
947

g. *Supraoccipital cartilage.*

1. The supraoccipital cartilage bears a very large anteriorly directed cartilaginous wing.
2. The tectum posterius chondrifies from two definite supraoccipital centres —one on each side.
3. The anteriorly directed wing of the supraoccipital does not chondrify from a separate centre.
4. The anterior wing of the supraoccipital cartilage displays, in later development, an autogenous ossification centre which gives rise to the adult "tabular".
5. Separate ossification centres for the "interparietal" could not be made out.

h. *Membrane bones.*

1. The premaxilla displays a well-defined processus prevomeralis which, however, has no separate ontogenetic identity.
2. In the adult golden mole the premaxillae are fused with each other and with neighbouring bony elements.

3. The maxilla, in later development, fuses with its fellow from the opposite side and with all the adjoining bony elements.
4. The very long zygomatic process of the maxilla, which forms the complete zygomatic arch, ossifies from a separate centre. It seems to imply that this process actually represents the missing jugal.
5. The lacrimal bone is present but it is not pierced by the lacrimal canal. It fuses later on with neighbouring bony elements.
6. The palatines in later development, fuse with each other and with the maxillae only.
7. The vomer arises from an unpaired median centre and in later life becomes inseparably fused with the ethmoid. It does not invade the anterior paraseptal cartilages.
8. The pterygoid, in its early development, arises from a single centre and displays a well-defined pterygoid cartilage. In the latest stage investigated it was found to be still completely separate from all other bony elements, and also from the ala temporalis.
9. The nasals fuse with each other and with neighbouring elements.
10. The frontal arises from a single centre and, in later development, fuses with all the adjoining bony elements.
11. The parietal likewise fuses with all the neighbouring bones.
12. The squamosal lacks a zygomatic process as well as a processus postglenoideus. It displays a poorly-defined glenoid cavity and, in the adult, contributes to the formation of the osseous bulla. It arises ontogenetically from a single centre.
13. The tympanic bone plays an important part in the formation of the osseous bulla. It arises from a single centre.
14. The preparticular invades the neck of the malleus as usual. It bears a small posteriorly directed spur which occupies the position of the surangular of other authors. This spur, however, has no separate identity; neither anatomically nor developmentally.

VOL. 28 194

PART IV. SETIFER SETOSUS (SCHREB.).

I. INTRODUCTION AND ACKNOWLEDGMENTS.

The systematic position of the Centetidae (Tenrecidae) as primitive members of the typical Insectivores has never been questioned. In the distant past they were believed to be near allies of the Golden Moles, but already DOBSON (1883) emphasised some important differences which indicate the early phylo-

genetic separation of the Golden Moles and the Centetidae. Also BROOM (1916) arrives at the final conclusion that the Centetidae and the Golden Moles are no near allies; the Centetidae being typical primitive Insectivores and the Golden Moles belonging to an entirely different Order.

Setifer setosus dealt with in this present paper was first described from Madagascar by SCHREBER (1777) as *Erinaceus setosus*. The generic name was changed by FRORIEP (1806) to *Setifer*, with *Erinaceus setosus* (SCHREB.) as genotype. Various synonyms for this species has been subsequently employed and for an account of these the reader is referred to the "Checklist of African Mammals" by ALLEN (1939).

Another species frequently mentioned in the present paper and from which one embryo has been sectioned is *Echinops telfairi telfairi Martin*. The genus *Echinops* was established by MARTIN (1838) with *Echinops telfairi* from Madagascar as genotype.

For an account of the synonyms subsequently employed by various authors the reader is likewise referred to the work of ALLEN (1939).

Acknowledgments: I wish to express my sincere thanks to Dr. R. H. GOETZ of the Department of Surgery, University of Cape Town, who kindly supplied me with all the embryonic material used for this part of my investigation.

II. MATERIAL AND TECHNIQUE.

The embryonic material of both *Setifer setosus* and *Echinops telfairi*, as well as that of *Tenrec ecaudatus*, used for this present investigation has been collected from Madagascar in 1937. The embryos were fixed in alcohol. The heads of the older stages were decalcified in Ebner's solution, neutralized, dehydrated and embedded in paraffin wax. Transverse serial sections were cut at a thickness varying from 10 μ, in the younger, to 15 μ in the older embryonic stages. The sections were stained on the slides with Hansen's haematoxylin and eosin.

The crown-rump measurements of the embryos investigated were as follows:

Setifer setosus: 9 mm; 9.3 mm; 9.8 mm; 10.5 mm; 20.2 mm; 20.4 mm and 47.4 mm.

Echinops telfairi: 29.4 mm.

Tenrec ecuadatus: 39.2 mm.

The head of the 20.2 mm embryo of *Setifer setosus*, being at about its optimal stage of chondrification, was sectioned longitudinally and the median sagittal section of this series gave an accurate outline of the curvature of the central stem. This was employed as base-line for the lateral view reconstruction of the chondrocranium of the 20.4 mm embryo.

III. THE CHONDROCRANIUM.

For discriptive purposes the chondrocranium will be divided into the following parts: A, the central stem; B, its appendages; C, lateral structures; D, the commissures interconnecting these and E, the dorsal structures. This method of description was devised by FAWCETT (1917) and has been widely adopted by other authors since then.

A. THE CENTRAL STEM.

At its optimal stage of chondrification the central stem in Setifer forms a continuous cartilaginous structure the various regions of which merge into each other.

As in Centetes (LEIMGRUBER 1939) and most of the other Insectivores the central stem is almost straight displaying only a very slight ventral concavity. Opposite the hind end of the inconspicuous dorsum sellae the central stem bears a slight ventral convexity.

The planum basale (figs. 55 56), having the usual triangular shape common to Mammals, is fairly thick throughout and at this stage of development shows no trace of the chorda dorsalis. Its extensive base forms the anterior margin of the foramen magnum and merges into the pila occipitalia laterally with a single pair of hypoglossal foramina as landmarks.

The apical portion of the basal plate is thicker than the rest and also much narrower, but it is not nearly as constricted as the corresponding part of the basal plate in Tupaia (HENCKEL 1928), Elephantulus and Eremitalpa (Author).

A fairly extensive jugular foramen and basicochlear fissure separates the middle and apical portions of the basal plate from the cochlear capsule. The basicochlear fissure is markedly convex laterally. Peculiar is the absence of a true posterior basicochlear commissure. In this region the lateral margin of the basal plate is closely applied to the cochlear capsule but a narrow strand of connective tissue intervenes so that no cartilaginous continuity is established between these structures; the basicochlear fissure would thus be confluent with the jugular foramen but for this intervening connective tissue.

The lamina hypophyseos (Pars trabecularis of FAWCETT and lamina polaris of other authors), in Setifer, has the shape of a wide transversely placed rectangle (figs. 55, 56). It lies medial to the carotid foramina and is much wider than the apical portion of the planum basale with which it is blended. In its anterior mid-dorsal aspect the lamina hypophyseos displays a shallow groove, indicating the position of the fenestra hypophyseos, which, however, is completely obliterated at this stage. From the antero-lateral border of the lamina hypophyseos the processus alaris arises and connects this plate with

the anterior end of the alicochlear commissure and with the basal end of the ala temporalis. The alicochlear commissure is complete. The entire absence of an anterior basicochlear commissure (Posterior trabeculocochlear commissure of FAWCETT), results in a confluency of the carotid foramen and basicochlear fissure.

As in most Insectivores the fossa hypophyseos is barely visible due to the absence of the tuberculum sellae and the very poor development of the dorsum sellae.

The trabecular plate (Pars Interorbitonasalis of FAWCETT) has the shape of a stout rod in its posterior part. It is fused with the lamina hypophyseos behind, and in this region is slightly flattened dorso-ventrally, but as it enters the intra-narial region it becomes compressed laterally to form the nasal septum. This part of the trabecular plate will be described in detail with the nasal capsule.

The common stem for the pre- and post optic roots of the ala orbitalis springs from the lateral border of the posterior part of the trabecular plate.

1. Early development of the Central Stem: The central stem is still entirely blastematous in the 9 mm embryo. At this stage the blastematous pars trabecularis is separated from the lamina hypophyseos by a fairly wide strand of undifferentiated mesenchyme. The lamina hypophyseos is a continuous blastem plate which shows no signs of either "polar elements" or a fenestra hypophyseos. The future processus alaris is poorly defined in blastem and communicates with the blastematous ala temporalis. Posteriorly the lamina hypophyseos ends dorsal to the anterior end of the blastematous planum basale.

The planum basale is well-defined in blastem and separated from the auditory capsule by a clearly distinguishable basicapsular fissure. Postero-laterally it is in strong blastematous continuity witht the blastem centres of the exoccipitals.

In the 9.3 mm embryo the pars trabecularis is slightly chondrified in its greater part only the anterior tip being still blastematous. At this stage it is still demarcated from the slightly chondrified lamina hypophyseos by a strand of dense blastem; actual cartilaginous continuity between the pars trabecularis and lamina hypophyseos is not established until after the 9.8 mm stage. In the 9.3 mm embryo the pars trabecularis is joined laterally by a procartilaginous pre- and a blastematous post-optic root of the ala orbitalis. Both these roots are in cartilaginous continuity with the pars trabecularis in the 9.8 mm embryo.

The lamina hypophyseos forms a continuous, slightly chondrified plate in the 9.3 mm embryo. Posteriorly it is in slight cartilaginous continuity with the planum basale. Both the processus alaris and the alicochlear commissure are still densely blastematous at this stage.

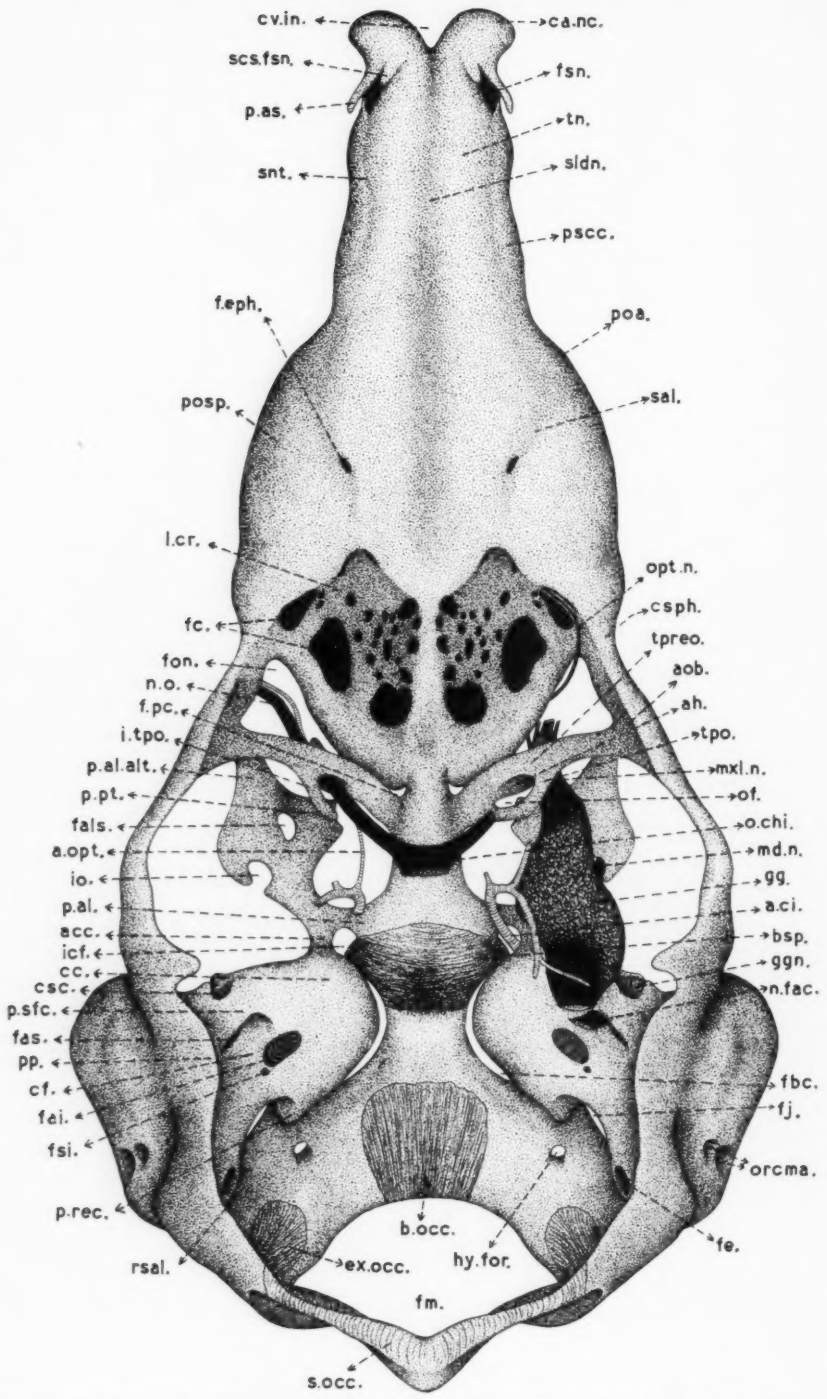

Fig. 55. Dorsal view reconstruction of the chondrocranium of a 20.4 mm embryo of S. setosus, indicating the position of ossification centres present, and the relations of a few important nerves and vessels (× 15).

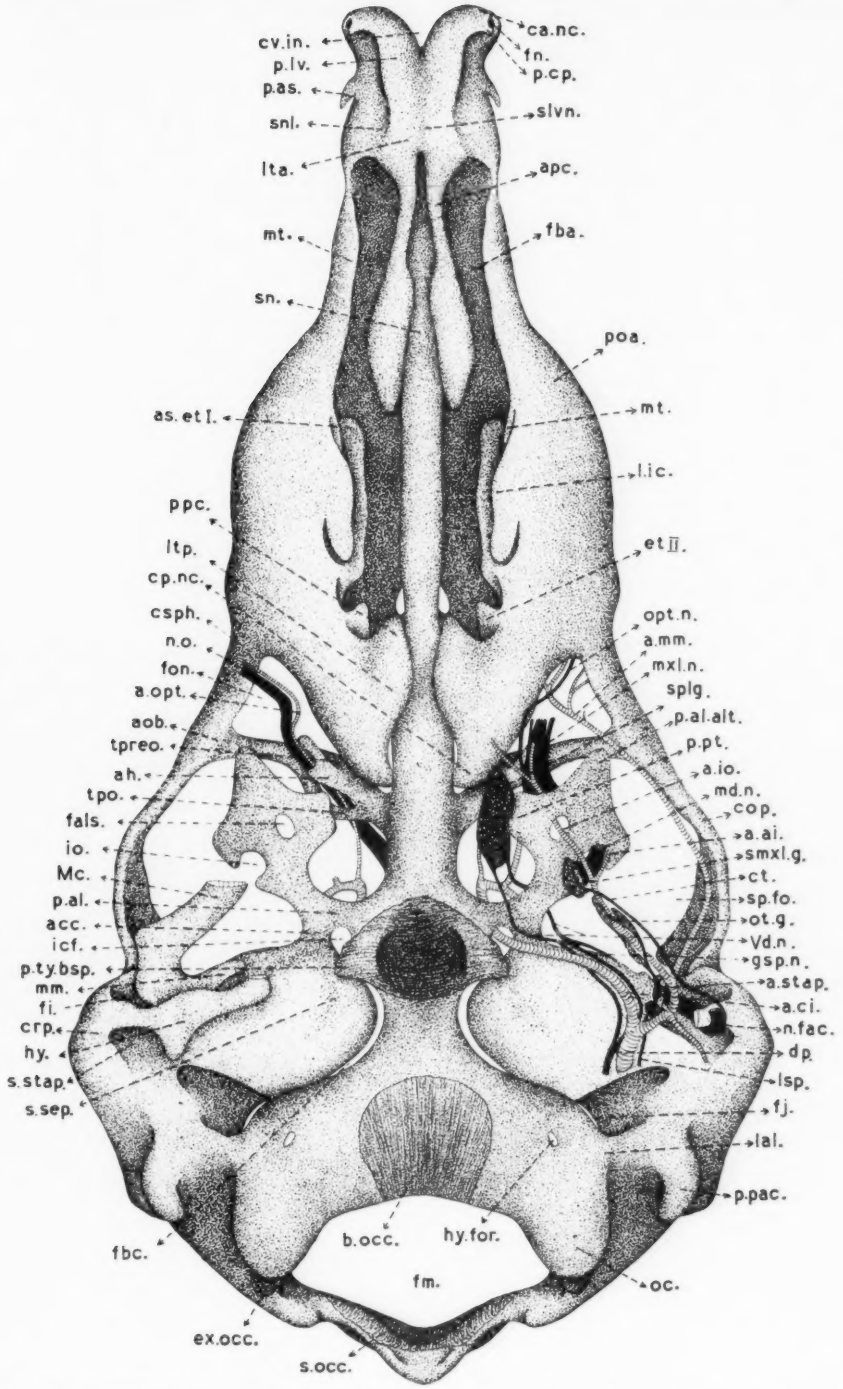

Fig. 56. Ventral view reconstruction of the chondrocranium of a 20.4 mm embryo of S. setosus, indicating also the position of ossification centres and the relations of some vessels and nerves (× 15).

In the 9.8 mm embryo the processus alaris is slightly chondrified as is also the anterior end of the alicochlear commissure, its posterior end being still blastematous. Both the processus alaris and the alicochlear commissure, therefore, chondrify in continuity with the lamina hypophyseos. In the 10.5 mm stage cartilaginous continuity is established between the pars trabecularis and the lamina hypophyseos; the alicochlear commissure is complete. Noteworthy is the very early obliteration of the fenestra hypophyseos as in the Golden Mole and Elephantulus.

The planum basale is already slightly chondrified in the 9.3 mm embryo and fairly well chondrified in the 9.8 mm embryo. In these stages it displays an elongated posterior basicranial fenestra which divides the basal plate into two parachordal plates, joined only at their anterior and posterior extremities. This fenestra is completely obliterated in the 10.5 mm embryo. At this stage a well-defined, but still procartilaginous, anterior absicochlear commissure is present, the posterior commissure being still deficient. Cartilaginous continuity between the planum basale and exoccipital is established at a very early stage, being well defined in the 9.3 mm embryo.

The notochord in the 9 mm embryo lies dorsal to the blastematous planum basale but its recurved anterior end pierces the extreme posterior tip of the blastematous lamina hypophyseos. When the basal plate chondrifies the notochord remains dorsal to it. In the 10.5 mm embryo it is complete and lies superficial (dorsal) to the planum basale in its entire extent. This retrobasilar type of notochord (Tourneux) is the most primitive, according to Matthes (1923) and is found in the Monotremes (Gaupp 1908, de Beer and Fell 1936) as well as in Mus and Xerus (Fawcett 1923) and Suncus (Author).

2. Post-optimal changes in the Central Stem: In the 20.4 mm embryo the planum basale already shows a fairly extensive but very slight perichondral ossification which represents the beginning of the basioccipital. This bone thus develops from a single centre in the planum basale anterior to the foramen magnum. In the oldest embryonic stage investigated (47.4 mm) the basioccipital is well ossified, and contributes to the formation of the most anterior and ventral tip of the occipital condyle. At this stage it is still separated by cartilage from the exoccipitals and from the basisphenoid.

The 20.4 mm embryo also displays a fairly well developed basisphenoid in the region of the lamina hypophyseos. Although only perichondral in nature it bears a pair of a small tympanic wings directed downwards and laterally and overlapping the basicochlear fissure ventrally in the position of the deficient anterior basicochlear commissure (fig. 56). Already at this early stage of development the anterior margin of the processus tympanicus basisphenoidei is fused with the posterior tip of the pterygoid. During later development the basisphenoid fuses with the alisphenoid as is already the case in the 47.4 mm

embryo. Its tympanic wings also increase greatly in size, extending over the entire length of the ventro-lateral margin of the basisphenoid and meeting the tympanic ring laterally.

WEBER (1928) regards the presence of a processus tympanicus basisphenoidii as characteristic of the Insectivores. It has also been described in Macroscelides (VAN DER KLAAUW 1929, KEEN and GROBBELAAR 1941) and in the Golden Mole (Author).

The presphenoidal region of the pars trabecularis is not yet ossified in the 47.4 mm stage but is already slightly encroached upon by the orbitosphenoids.

A mesethmoid ossification centre could be clearly distinguished in the 47.4 mm embryo but it will be discussed in more detail with the nasal capsule.

A 29.4 mm embryo of *Echinops telfairi* which was also sectioned showed a basioccipital and basisphenoid not at all unlike those described for *Setifer setosus* but a separate mesethmoid ossification centre could not be made out in this stage.

OL.
28
947

B. LATERAL STRUCTURES APPENDED TO THE CENTRAL STEM.

These include the exoccipital cartilages (pilae occipitales), the auditory capsules, the alae temporales, the alae orbitales and the nasal capsules. (The foramina between these structures and the central stem will be discussed with the structure concerned.)

1. The exoccipital cartilages (figs. 56, 59, 60) are massive. Each one is fused below with the basal angle of the planum basale. The hypoglossal foramen, which indicates the site of union, lies medial to the posterior end of the jugular foramen as in Tupaia (HENCKEL 1928), Erinaceus (FAWCETT 1918) and Primates.

Antero-ventrally the processus alaris of the exoccipital is in weak synchondrotic continuity with the ventro-lateral aspect of the pars canalicular posterior to the jugular foramen. The processus paracondyloideus is massive and ends behind in a blind pointed extremity.

The recessus supra-alaris, which lodges the terminal part of the sigmoid sinus, is wide and separates the pars canalicularis from the bulk of the exoccipital. Posteriorly the recessus supra-alaris is continued into the lower end of the occipito-capsular fissure. A posterior occipito-capsular commissure which, when present, joins the cupula posterior of the pars canalicularis to the exoccipital cartilage is absent; the fissura occipito-capsularis superior (fissura capsulo-parietalis or foramen jugulare spurium) and the fissura occipito-capsularis inferior (posterior) are therefore confluent.

Antero-superiorly the exoccipital cartilage merges insensibly into the parietal plate, while postero-superiorly it is fused with the supraoccipital. This latter

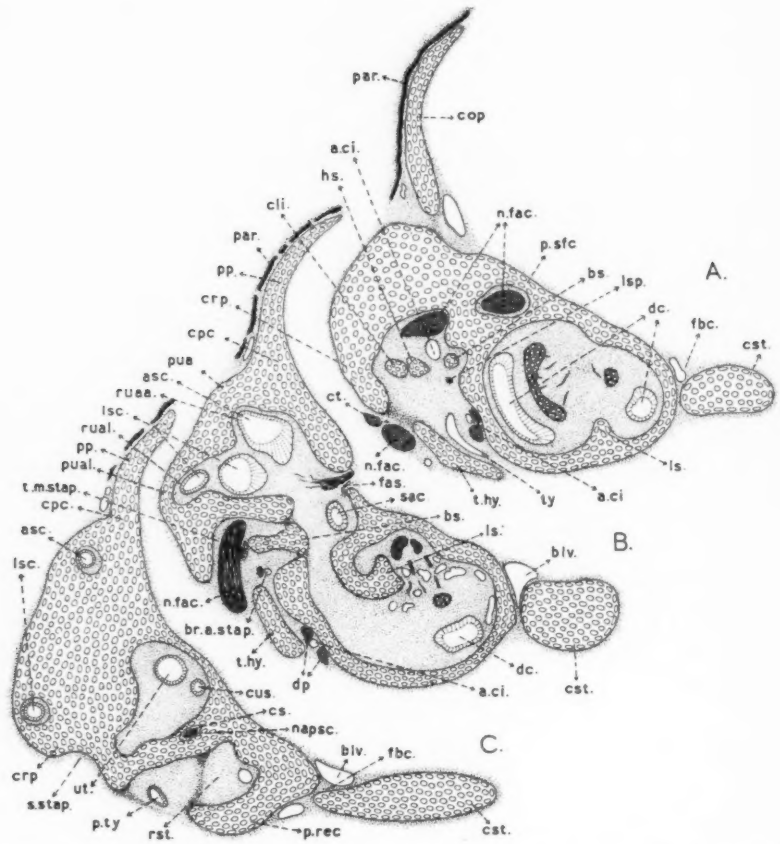

Fig. 57 A—C. Consecutive transverse sections through the auditory capsule of a 20.4 mm embryo of S. setosus (× 17.5).

line of fusion, however, can be easily detected even at this relatively advanced stage of development, since its position is indicated by a strand of very much flattened and compressed cartilage cells. The exoccipital cartilage bounds the foramen magnum laterally and forms the greater part of the large and well-defined occipital condyle.

a. *Early development of the exoccipital cartilage:* In the 9 mm embryo the exoccipital is densely blastematous and in strong continuity with the planum basale. In the 9.3 mm embryo it is well-defined in young cartilage and is already in cartilaginous continuity with the slightly chondrified planum basale. An autogenous centre of development for the exoccipital could therefore not be made out, neither in blastem nor in cartilage. The blastem rudiment of the supraoccipital is still separate from the exoccipital in the 9.3 mm embryo. Similarly the two cartilages are separate in the 9.8 mm stage, and only in the

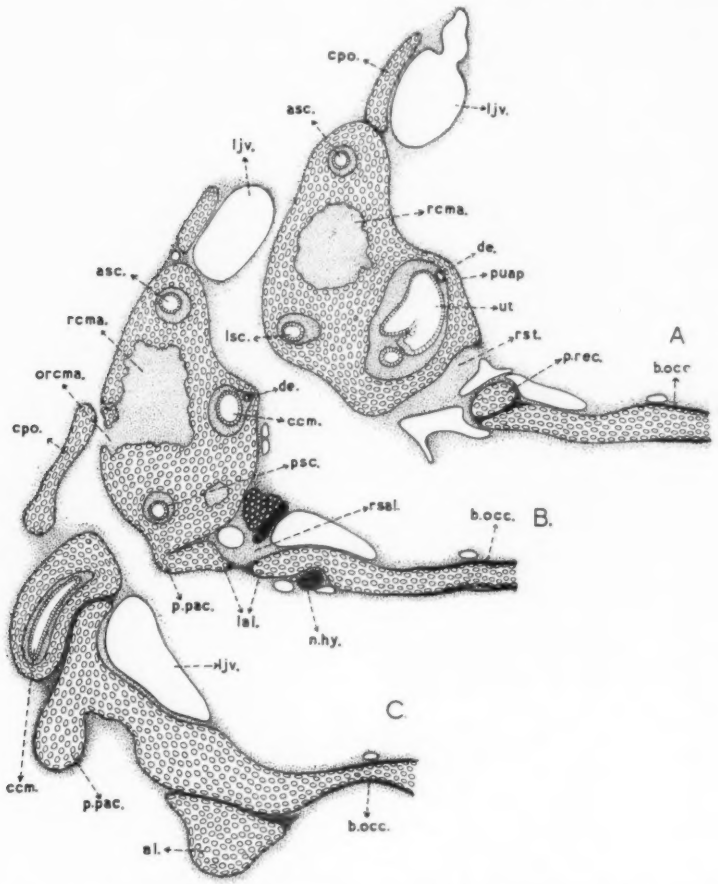

Fig. 58 A—C. Consecutive transverse sections through the posterior part of the auditory capsule of a 20.4 mm embryo of S. setosus (× 17.5).

10.5 mm embryo is cartilaginous continuity established between the ex- and supraoccipitals. The lamina alaris and the paracondyloid process of the exoccipital are the last portions to develop. In the 10.5 mm embryo the connections of the lamina alaris to the pars canalicularis are still blastematous, while the paracondyloid process is hardly developed.

b. *Post-optimal changes in the exoccipital cartilage:* The 20.4 mm embryo displays a fairly extensive perichondrally ossified exoccipital cartilage. In the 47.4 mm embryo this ossification involves the greater part of the exoccipital cartilage excluding only the tip of the paracondyloid process and narrow strands of cartilage intervening between it and the basi- and supraoccipital ossifications. The exoccipital forms by far the greater part of the occipital condyle, and at this stage the hypoglossal canal is only partly enclosed in it.

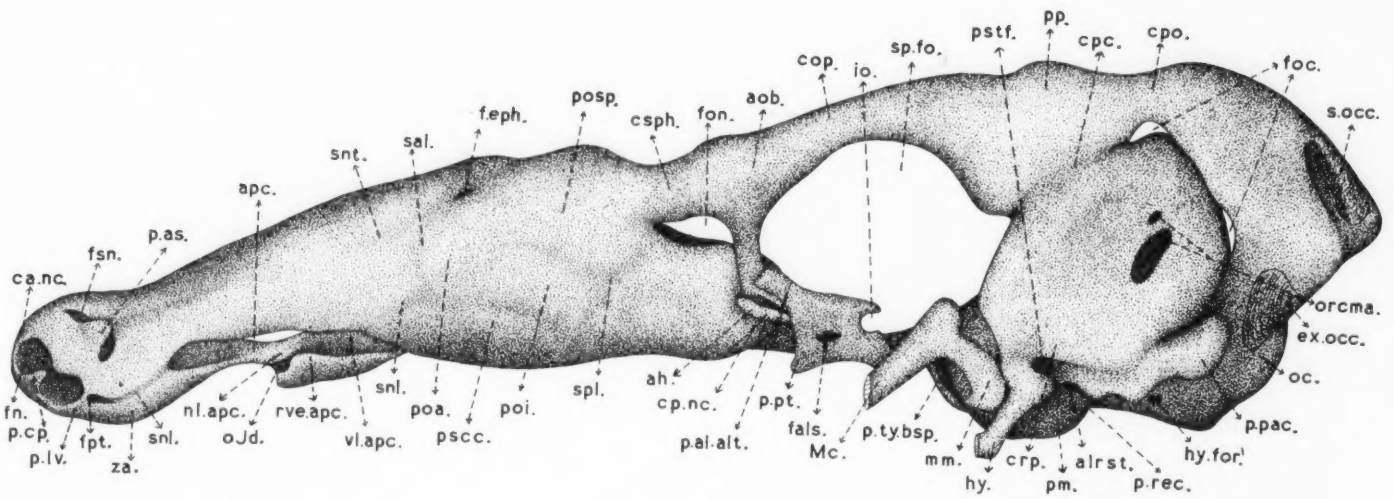

Fig. 59. Lateral view reconstruction of the chondrocranium of a 20.4 mm embryo of S. setosus (× 15).

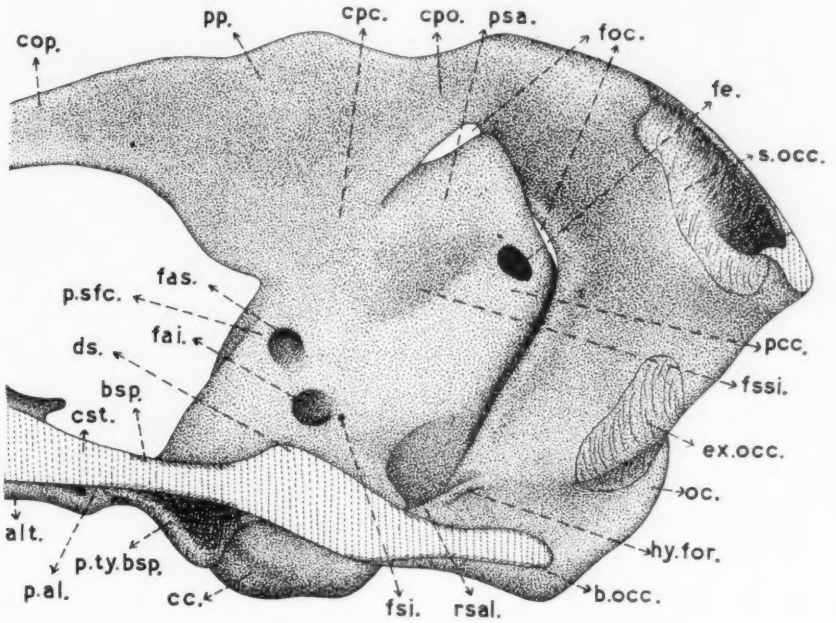

Fig. 60. Medial view reconstruction of the otic and occipital regions of the chondrocranium of a 20.4 mm embryo of S. setosus (× 22.5).

2. The Auditory Capsule (figs. 55—60) can be divided into the pars canalicularis (pars posterior), which lodges the utricle and the semicircular canals and the pars cochlearis (pars anterior), which lodges the saccule and the ductus cochlearis.

The auditory capsule of Setifer is markedly quadrilateral in shape, the pars canalicularis being highly elevated above the plane of the planum basale. The long axis of the auditory capsule is directed forwards, downwards and medially so that the two cochlear capsules converge and constrict the anterior part of the planum basale; not to the same extent, however, as in Tupaia, Elephantulus and Eremitalpa. A relatively small portion of the cochlear capsule projects downwards below the plane of the planum basale.

Most of the connections of the auditory capsule to neighbouring parts of the chondrocranium have already been mentioned. They are as follows: the pars cochlearis is attached to the central stem only indirectly by means of the alicochlear commissure, since both the anterior and posterior basicochlear commissures are deficient. The ventro-lateral aspect of the pars canalicularis is in weak synchondrotic continuity with the lamina alaris of the exoccipital cartilage and for the rest its antero-dorsal aspect is joined to the parietal plate by the anterior capsulo-parietal commissure.

The parietal plate is strongly developed. It is sagittally placed with a slight

dorso-medial inclination and a pronounced medially-facing concavity. Anteriorly it is attached to the ala orbitalis by the orbito-parietal commissure, posteriorly it communicates with the occipital cartilages through the occipito-parietal commissure and ventrally it attaches to the antero-dorsal aspect of the pars canalicularis by the anterior capsulo-parietal commissure. The lateral jugular vein runs backwards medial to this latter commissure.

The processus opercularis is absent.

The tegmen tympani is absent, but its position is indicated by an extremely slight, rounded, anterior thickening of the crista parotica.

The crista parotica is massive. The upper end of the tympano-hyale attaches to its ventral border anterior to the primary stylomastoid foramen. At its attachment to the crista parotica the tympano-hyale displays a deep posterior incisure for the facial nerve and a slight anterior incisure for the chorda tympani nerve. Behind the attachment of the tympano-hyale the crista parotica is continued as a massive ridge dorso-lateral to the well-defined sulcus musculi stapedii.

The pars canalicularis of the auditory capsule is roughly quadrilateral in shape. Its medial surface is peculiar in that the semicircular canals hardly stand out in relief; as a consequence the fossa subarcuata superior interna, although noticeable, is not well defined, while a fossa subarcuata inferior (posterior) interna can hardly be distinguished. The prominentia utriculo-ampullaris posterior (inferior), however, stands out in bold relief.

From the antero-medial end of the pars canalicularis the strongly developed suprafacial commissure arches forwards, downwards and medialwards to the anterior dorso-lateral aspect of the cochlear capsule, thus enclosing the primary facial foramen. Antero-lateral to the suprafacial commissure lies a small but well-defined cavum supracochleare (hiatus spurius) which lodges the bulk of the geniculate ganglion. Laterally this cavity is bordered by an anteriorly directed cartilaginous spur which springs from the antero-dorsal aspect of the pars canalicularis and the anterior end of which is closely applied to a faint ridge on the antero-lateral aspect of the cochlear capsule. This spur bridges over the foramen faciale secundarium through which the bulk of the facial nerve leaves the cavum supracochleare to enter the sulcus facialis.

The lateral surface of the pars canalicularis is for the greater part uniformly convex, there being rather a prominentia than a fossa subarcuata superior externa. As a result of this and of the poor development of fossae on the medial surface of the pars canalicularis the cartilage interposed between the semicircular canals would have been massive had it not been for a secondary hollowing-out of the pars canalicularis. A fairly extensive but highly irregularly shaped cavity occupies the bulk of the massa angularis and intervenes between the anterior and posterior semicircular canals. This cavity does not communicate with the cavum cranii but communicates with the exterior by

VOL
28
194

means of a couple of irregularly-shaped openings on the lateral surface of the pars canalicularis.

The pars cochlearis can be divided for descriptive purposes into a vestibular segment containing the saccule and a cochlear segment which contains the cochlear duct. The vestibular segment is interposed between the pars canalicularis and the cochlear capsule. Laterally the sulcus facialis and the sulcus musculi stapedii delimit it from the pars canalicularis. Medially there are hardly any recognisable landmarks demarcating it from the adjoining parts of the auditory capsule.

The cochlear segment ends in front in the cupula anterior which is situated behind the carotid foramen. Its dorsal intra-cranial surface is smooth and convex. Its ventral and ventro-lateral extra-cranial surfaces are more pronounced convex, displaying a well defined sulcus septalis ventro-medially and an equally well-defined sulcus for the internal carotid artery and deep petrosal nerve ventro-laterally.

VOL. 28 1947

a. *Foramina in the wall of the auditory capsule:* The meatus auditorius internus, lying in the dorso-medial wall of the vestibular segment, leads into the primary facial foramen anteriorly. Laterally it leads into the foramen acusticum superius, which transmits branches of the auditory nerve to the utricle, ampullae of the anterior and lateral semicircular canals and to part of the saccule. Postero-medially it leads into the foramen acusticum inferius which transmits branches of the auditory nerve to the cochlea, part of the saccule and to the ampulla of the posterior semicircular canal, the latter nerve fibres being enclosed in a separate foramen singulare; no separate foramen for the lower nerve to the saccule is isolated.

The foramen endolymphaticum is a simple, oval-shaped foramen in the medial wall of the prominentia cruris communis relatively far back and near its termination.

The processus recessus in Setifer displays primitive relations. It projects backwards as a continuation of the floor of the pars cochlearis but it ends freely behind not being fused to the floor of the posterior part of the pars canalicularis as is usually the case in Mammals.

The processus recessus is not slender and rod-like as in the mouse (DE BEER) but has the shape of a wide plate, tapering backwards and slightly concave above, it rests on, but is not fused with, the lateral edge of the planum basale.

A somewhat similar condition has been reported to obtain in the cat (TERRY 1917 and DE BEER 1929). As a result, the recessus scalae tympani is still partly extracapsular in Setifer and neither its apertura lateralis (fenestra rotunda) nor its apertura medialis is completely isolated. Where the processus recessus ends behind, the apertura medialis of the recessus scalae tympani is confluent with the jugular foramen. The foramen perilymphaticum through

which the ductus perilymphaticus enters the recessus scalae tympani, displays the normal relations characteristic for Mammals.

The fenestra ovalis, apart from its being exceptionally small, displays normal Mammalian relations.

b. *The interior of the Auditory Capsule:* As is always the case in Mammals the cavum vestibulare, lying between the cavum canaliculare and cavum cochleare, communicates freely with the anterior part of the cavum canaliculare dorso-laterally. The anterior part of the cavum vestibulare is completely separated from the cavum cochleare by the basal portion of the septum spirale, which is fused to the ventral aspect of the crista falciformis.

The septum spirale is well developed and its attachment to the cochlear capsule results in the formation of the well-defined sulcus septalis externally.

The posterior portion of the cavum vestibulare is only partly delimited from the cavum cochleare by the well-defined ridge running along the ventro-lateral side of the dorso-medial wall of the pars cochlearis, from behind the foramen acusticum inferius to the antero-medial end of the posterior border of the foramen perilymphaticum.

The nerve to the ampulla of the posterior semicircular canal, which enters the auditory capsule through the foramen singulare, runs backwards lateral to this ridge, contained in a deep groove and in parts in a tunnel in this ridge. Somewhat similar relations have been described for Elephantulus (Author).

The posterior portion of the cavum cochleare becomes the cavum perilymphaticum and recessus scalae tympani.

Whereas the anterior part of the cavum canaliculare lacks a floor and communicates freely with the cavum vestibulare, as it has already been described, its posterior part has a complete floor which roofs the recessus scalae tympani and the free anterior edge of which forms the true posterior delimitation of the foramen perilymphaticum.

c. *Early development af the auditory capsule:* The auditory capsule is entirely blastematous in the 9 mm embryo, but displays two definite blastem concentrations: one in the pars cochlearis and another in the pars canalicularis—the pars vestibularis being more poorly defined in blastem.

In the 9.3 mm embryo the auditory capsule is still densely blastematous, but in the 9.8 mm stage it is slightly chondrified in the pars cochlearis and pars canalicularis, the junctional zone between these centres, i.e. the walls of the pars vestibularis, being still to a large extent densely blastematous or slightly procartilaginous in parts. In the 10.5 mm stage the entire auditory capsule is more or less chondrified, except for the dorsomedial wall of the cavum vestibulare, including the crista falciformis.

Regarding the connections of the auditory capsule to neighbouring parts of the chondrocranium, the alicochlear commissure is completely chondrified in the 10.5 mm embryo, the anterior basicochlear commissure is still pro-

VOL
28
194

cartilaginous at this stage, being entire deficient again in the 20.4 mm embryo; the posterior basicochlear commissure is deficient in the 10.5 mm stage, this being still the case in the 20.4 mm embryo; the connection between pars canalicularis and lamina alaris of the exoccipital does not chondrify until some time after the 10.5 mm stage, being only slightly chondrified in the 20.4 mm embryo.

The parietal plate in the 9.3 mm embryo is densely procartilaginous but its connections with the auditory capsule and the ala orbitalis are still blastematous at this stage, while the occipito-parietal commissure is still completely deficient.

In the 9.8 mm embryo the parietal plate is slightly chondrified and in cartilaginous continuity with the auditory capsule. Cartilaginous continuity between it and the ala orbitalis and supraoccipital, however, is not established until in the 10.5 mm stage and even then the occipito-parietal commissure is only extremely slender.

The primary facial foramen is well defined in cartilage in the 10.5 mm embryo, but the secondary facial foramen is non existent.

Contrary to the usual procedure, the poorly developed processus recessus develops rather early in ontogeny, being already present and slightly chondrified in the 9.8 mm embryo.

d. *Post optimal changes in the auditory capsule:* These changes could not be traced in any detail due to the lack of suitable embryonic stages, therefore only the changes noticed in a 47.4 mm embryo will be discussed.

The 47.4 mm embryo displayed a complete foramen faciale secundarium for the exit of the facial nerve from the cavum supracochleare.

The processus recessus has still the shape of a thick plate tapering to a blind end behind, but in addition, a slender cartilaginous spur is found in this stage, extending backwards and medially from the lower lateral surface of the pars canalicularis in front to the postero-lateral edge of the processus recessus behind. This cartilage spur isolates a fenestra rotunda laterally but does not render the recessus scalae tympani intracapsular as yet; neither does it delimit the apertura medialis of the recessus scalae tympani from the extensive foramen jugulare, so that the fissura metotica still retains its primitive undivided form.

At this stage the auditory capsule displays three more or less welldefined ossification centres. The one centre occupies the antero-lateral part of the vestibular segment and pars canalicularis, involving the whole area round the cavum supracochleare, the roof of the fossa incudis and anterior end of the fenestra ovalis.

Another extensive centre occupies the postero-medial part of the cochlear capsule, involving the processus recessus, the area round the apertura medialis of the recessus scalae tympani and the roof of the cochlear capsule postero-medial to the foramen acusticum inferius. This ossification centre is already

partly blended with another in the postero-medial wall of the pars canalicularis, where it involves the prominentia utriculo-ampullaris posterior (inferior) and the prominentia cruris communis.

A 29.4 mm embryo of *Echinops telfairi* also showed these three ossification centres well defined, and they appear to be more or less characteristic of Mammals, having been found also in Suncus, Elephantulus and Eremitalpa (Author).

No rostral or caudal entotympanics or rostral or caudal petrosal tympanic plates were found in Setifer.

3. The ala temporalis (figs. 55, 56 and 59) in Setifer is a fairly extensive plate, roughly quadrilateral in shape and lying at an angle of about 40° to the horizontal plane. It is joined to the extreme antero-lateral edge of the lamina hypophyseos by the processus alaris and to the cupula anterior of the cochlear capsule by the alicochlear commissure. Its so-called antero-lateral process which, in Mammals, is often pierced by the mandibular nerve, is an extensive plate the anterior end of which extends as far forwards as the ala orbitalis. In its postero-lateral aspect this plate displays a deep incisura ovalis which transmits the mandibular nerve. A similar incisura, instead of a foramen ovalis, has been described for Tupaia (HENCKEL 1928) and in Elephantulus (Author). At about its centre the ala temporalis is pierced by the foramen alisphenoidale which transmits the infraorbital artery. Similar conditions have been reported for: Ornithorhynchus (WATSON 1916, DE BEER and FELL 1936), ox (ARNOLD 1928) and Elephantulus (Author).

The pterygoid process (anterior process of FAWCETT) of the ala temporalis is directed antero-medially. It is fairly broad, but short, and it bears no intimate relations either with the pterygoid cartilage or with the pterygoid bone. Between the pterygoid process and the antero-lateral process the antero-medial surface of the ala temporalis displays a wide and shallow notch which transmits the maxillary division of the trigeminal nerve.

a. *Early development of the ala temporalis:* The ala temporalis in the 9 mm embryo is represented by a local blastem centre, which, in the 9.3 mm embryo is still unchondrified but in strong blastematous continuity with the lamina hypophyseos by means of a densely blastematous processus alaris. The 10.5 mm embryo presents a local chondrification centre in the ala temporalis, which, at this stage, is still separated from the central stem by a strand of procartilage in the basal end of the ala temporalis. No separate chondrification or blastem centre could be made out for the pterygoid process of the ala temporalis.

b. *Post optimal changes in the ala temporalis:* As usual, the ala temporalis ossifies to form the alisphenoid of the adult skull. The exact position of this ossification centre and the stage at which it first appears could not be determined for the lack of embryonic material.

In the 47.4 mm embryo the alisphenoid was found to be extensively ossi-

VOL
28
194

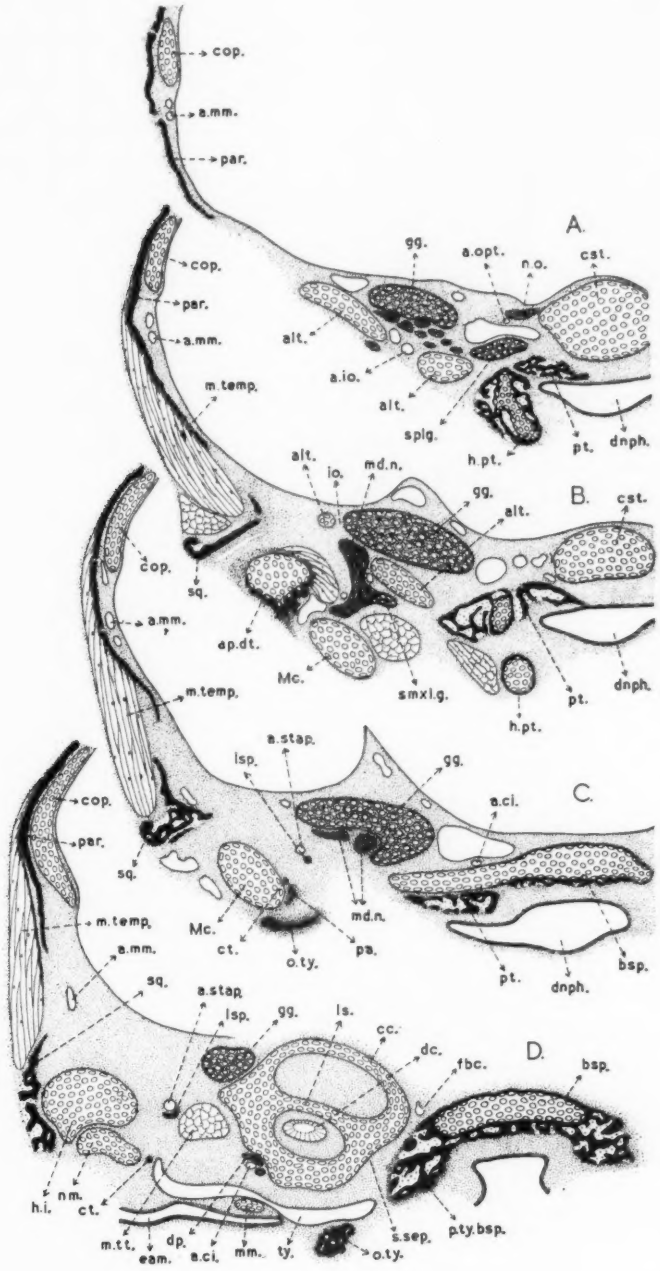

Fig. 61 A—D. Consecutive transverse sections through the posterior sphenoidal region of the head of a 20.4 mm embryo of S. setosus (× 30).

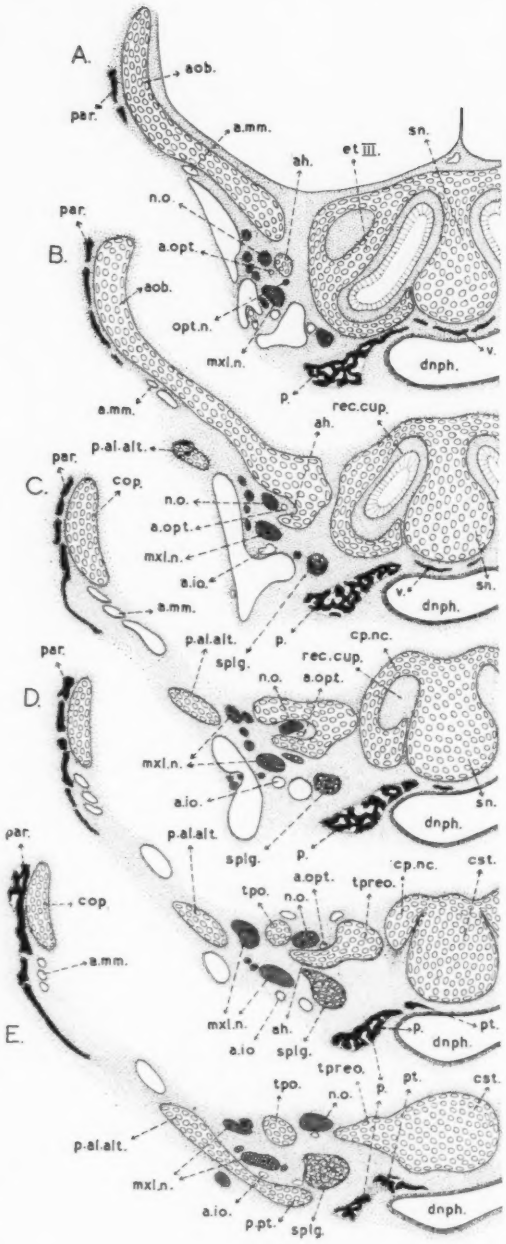

Fig. 62 A—E. Consecutive transverse sections through the anterior sphenoidal region of the head of a 20.4 mm embryo of S. setosus (× 30).

fied. It involves the entire anterior and lateral parts of the ala temporalis leaving only the small postero-medial basal end of the ala temporalis cartilaginous; even this cartilaginous portion is slightly perichondrally ossified so that, already at this stage, the alisphenoid and basisphenoid ossifications are fused. Furthermore, the posterior end of the pterygoid is fused with the alisphenoid near its basal end in the 47.4 mm embryo. The alisphenoid ossification at this stage is pierced by two foramina: one, the alisphenoid canal, transmits the infraorbital artery while the other, the foramen ovale, transmits the mandibular nerve. The alisphenoid is related to the palatine: pterygoid, orbitosphenoid, parietal, squamosal, tympanic and basisphenoid.

4. The ala orbitalis (Figs. 55, 56, 59, 62) in Setifer is rather slender and rodlike if compared with the majority of other Mammals investigated. It forms the ventro-lateral protection for the anterior part of the brain and its upper anterior angle is connected to the pars intermedia of the nasal capsule by a well-defined spheneth-moidal commissure. Its upper posterior angle is joined to the anterior edge of the parietal plate by a well-developed orbito-parietal commissure, thus completely isolating the extensive spheno-parietal fontanella.

VOL.
28
947

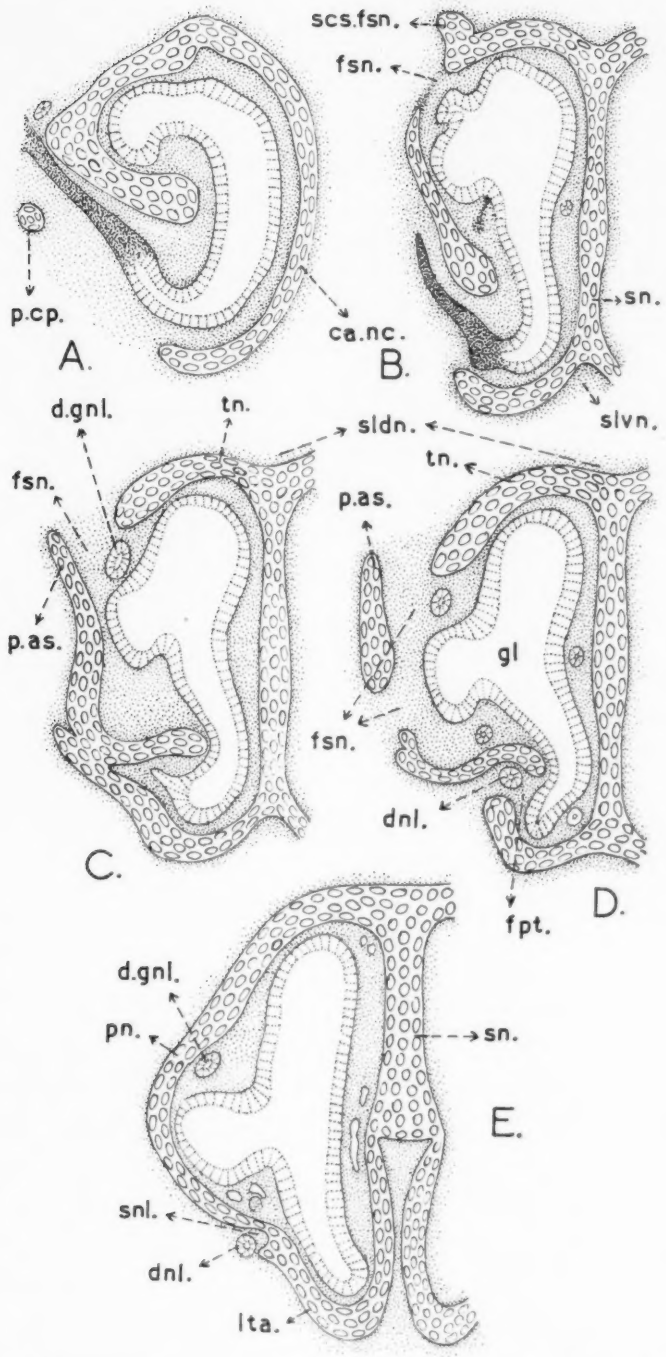

Fig. 63 A—E. Consecutive transverse sections through the most anterior end of the snout of a 20.4 mm embryo of S. setosus (× 50).

The apical portion of the ala orbitalis is directed downwards, medially and slightly backwards. It bifurcates to enclose the optic foramen between the pre- and post optic roots, these, after reuniting, join the trabecular plate by a short but fairly wide common stem. The post optic root is rather slender and is deficient on the one side of the specimen investigated. A deficient post optic root has been described in all Marsupials thus far investigated, and also in Microtus (FAWCETT 1917 and 1919) and in Galaeopithecus (HENCKEL 1929).

The pre-optic root is strongly developed and abuts against the postero-lateral aspect of the cupula posterior of the nasal capsule, thus delimiting a small medially placed foramen prechiasmaticum from the extensive dorso-lateral division of the orbito-nasal fissure.

The ala hypochiasmata is well defined and arises by a broad base from the posterior and ventral surfaces of the pre-optic root. It projects laterally and forwards and forms a shelf below the optic nerve and ophthalmic artery as these structures traverse the optic foramen.

a. *Early development of the ala orbitalis:* In the 9 mm embryo the ala orbitalis displays a well-defined autogenous blastem centre which does not communicate with the blastematous sphenethmoidal commissure but is already in slight blastematous continuity with the pars trabecularis by means of its pre-optic root; the post optic root is not defined in blastem as yet. In the 9.3 mm embryo the ala orbitalis is slightly chondrified but the sphenethmoidal commissure, the orbito-parietal commissure and the pre-optic root are still procartilaginous, while the post optic root is entirely blastematous.

The 9.8 mm embryo displays a well chondrified ala orbitalis with a well-defined ala hypochiasmata. All its connections to neighbouring parts of the chondrocranium are in cartilage, except for the orbito-parietal commissure which is still, in part, procartilaginous. In the 10.5 mm stage this commissure is also completely chondrified.

b. *Post optimal changes in the ala orbitalis:* As in the case of the alisphenoid the exact stage at which the ala orbitalis begins to ossify and the exact position of the centre(s) could not be determined for the lack of suitable embryonic stages.

In the 47.4 mm embryo the orbitosphenoid is an extensive ossification which is thick and strongly pneumatic. It involves the entire medial part of the ala orbitalis; due to extensive expansion in membrane bone fashion, it forms a cup-shaped investment for the cupula posterior of the nasal capsule. The orbitosphenoid, at this stage, displays a well-defined optic foramen and is related to the following bony elements: vomer, palatine, alisphenoid, frontal and pterygoid. The sphenethmoidal commissure is still intact, but the orbito-parietal commissure is almost completely resorbed.

As previously stated the presphenoidal region of the central stem is still unossified in the 47.4 mm embryo of Setifer. The postero-medial ends of the

VOL. 28 194

two orbitosphenoids, however, already encroach to a small extent on the presphenoidal region of the central stem in front of the basisphenoid.

It appears extremely unlikely that separate presphenoid ossification centres will still arise, and this region thus seems to await ossification spreading medialwards from the orbitosphenoids.

3. The nasal capsule (figs. 55, 56, 59, 63, 64), is strongly developed and its length amounts to slightly more than half the total length of the chondrocranium. Roughly one third of the nasal capsule is subcerebral, the remaining two thirds being precerebral.

Both internally and externally the nasal capsule can be divided into three parts, viz: pars posterior, pars intermedia and pars anterior. The boundaries of these parts will be described in due course.

Exterior of the nasal capsule: The tectum Nasi (fig. 55). The roof of the pars intermedia and pars poste-

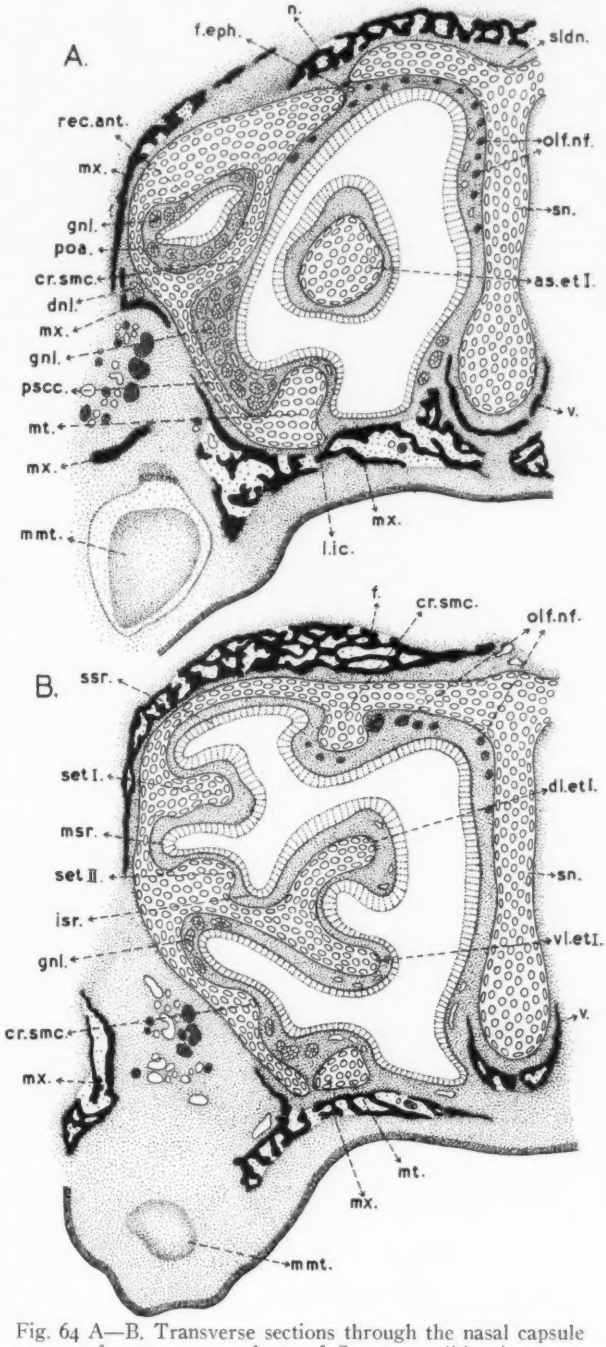

Fig. 64 A—B. Transverse sections through the nasal capsule of a 20.4 mm embryo of S. setosus (× 30).

rior of the nasal capsule is subcerebral in position and is formed almost exclusively by the lamina cribrosa. This part of the tectum nasi inclines backwards and downwards forming an angle of about 30° with the horizontal plane. It is well fenestrated, transmitting the fila olfactoria and part of the ophthalmic branch of the trigeminal nerve.

The medial borders of the two cribriform plates fuse with the postero-dorsal edge of the septum nasi, and although the septum and the medial parts of the two cribriform plates lie at a higher level than the lateral halves, one could hardly speak of a crista galli being present. Neither is the crista intercribrosa, which is supposed to divide the cribriform plate into an antero-lateral and a postero-medial part, at all well developed.

The tectum nasi posterius is well-defined and fused with the septum nasi medially. It is almost horizontal in position, not being as steeply inclined downwards and backwards as the cribriform plate.

The terminal part of the ophthalmic nerve enters the nasal cavity together with several bundles of olfactory nerve fibres through a large foramen in the most lateral part of the cribriform plate.

The pars anterior of the tectum nasi slopes gently downwards and forwards. Medially the tectum nasi is fused with the upper edge of the septum nasi and laterally it passes insensibly into the upper medial edge of the paries nasi. A small foramen epiphaniale is present. The sulcus dorsalis nasi, lying over the upper edge of the septum nasi is deepest towards the middle of the pars anterior. Near the anterior tip of the snout it rapidly increases in depth and leads into the cavum internasale between the cupulae anteriores of the nasal capsules.

The paries nasi (fig. 59) is complete in the posterior and middle divisions of the nasal capsule but displays several deficiencies in its anterior part. The pars posterior is delimited from the pars intermedia by the illdefined sulcus postero-lateralis which runs downwards and forwards and corresponds to the internal attachment of the middle and anterior roots of the first primary ethmoturbinal. The ventral edge of the pars posterior curves medially into the lamina transversalis posterior, while its dorsal edge is continued into the tectum nasi posterius and lamina cribrosa; posteriorly it leads into the cupula posterior of the nasal capsule.

The pars intermedia, being pushed outwards by the deep internal recesses of the nasal cavity projects far laterally and gives the nasal capsule its characteristic pear shape. Anteriorly the pars intermedia is delimited by the sulcus antero-lateralis, corresponding to the internal attachment of the crista semicircularis. On its outer surface the pars intermedia displays only one ill-defined sulcus which corresponds to the internal attachment of the long superior root of the first primary ethmoturbinal. This sulcus partly delimits the large prominentia superior (prominentia frontalis of FAWCETT) from the

prominentia anterior and the prominentia inferior (prominentia maxillaris of FAWCETT). The prominentia superior gives rise to the sphenethmoidal commissure postero-dorsally, but the internal attachments of the first and second secondary ethmoturbinals do not result in the formation of any secondary sulci on its smooth and convex outer surface.

The pars anterior is long but narrow. Posteriorly the sulcus antero lateralis delimits it from the pars intermedia. Dorsally it is continuously blended with the tectum nasi anterius. The posterior half of the inferior border of the pars anterior is thickened to form the maxilloturbinal and below the posterior part of this turbinal the paries nasi is continued into a narrow and ill-defined lamina infraconchalis, as in the rabbit (VOIT 1909) and water rat (FAWCETT 1917). Due to the pronounced anteriorly facing convexity of the sulcus antero-lateralis the greater part of the prominentia supraconchalis lies ventral to the prominentia anterior, instead of anterior to it. Dorsally the prominentia supraconchalis is delimited by a faint sulcus which corresponds to the attachment of the ill-defined nasoturbinal. A fairly well-developed sulcus for the naso-lacrimal duct crosses the prominentia supraconchalis from its antero-ventral to its postero-dorsal aspect, where it blends with the lower limb of the sulcus antero-lateralis.

The inferior border of the anterior third of the paries nasi is fused with the lateral edge of the lamina transversalis anterior, thus resulting in the formation of a complete zona annularis. The nasolacrimal duct runs forwards in a deep sulcus over the ventro-lateral aspect of the zona annularis. This sulcus is believed to indicate the junctional zone between paries and solum nasi in this region. Anteriorly the sulcus leads into a small foramen pretransversale through which the nasolacrimal canal enters the cavum nasi. The foramen pretransversale is delimited from the extensive fenestra naris by an extremely slender bar of cartilage which extends from the processus lateralis ventralis below, to the ventral edge of the paries nasi above. Postero-dorsal to the fenestra naris an extensive fenestra superior nasi (foramen dorsale, FAWCETT or fenestra lateralis, STURM) can be distinguished. This fenestra is separated from the fenestra naris by a wide strip of paries nasi which, in front of the fenestra superior nasi, joins the tectum nasi, thus contributing to the formation of the cup-shaped cupula anterior.

The processus alaris superior in Setifer is not very well defined. It has the shape of a small cartilaginous wing attached to the paries nasi, antero-ventral to the fenestra superior nasi. It projects upwards, backwards and sideways and bridges over the fenestra superior nasi. A strong muscle tendon attaches to its posterior tip.

From the ventro-lateral border of the cupula anterior a short cartilaginous spur, the processus cupularis, projects upwards, backwards and sideways. A

similar structure has been described in Erinaceus (FAWCETT 1918) and in Suncus (Author).

The fenestra naris is extensive and is bound as follows: Anteriorly by the cupula anterior, postero-dorsally by the paries nasi, ventrally by the processus lateralis ventralis and antero-laterally by the processus cupularis.

The solum nasi (fig. 56) in Mammals is always rather incomplete. In the pars posterior of the nasal capsule in Setifer the floor is almost complete, being formed for the greater part by the lamina transversalis posterior. This lamina is supplemented by the posterior paraseptal cartilage which, postero-laterally and posteriorly, merges into the lamina transversalis posterior. The posterior paraseptal cartilage projects forwards from the lamina transversalis posterior as a short blunt process. A narrow septo-paraseptal fissure intervenes between the posterior paraseptal cartilage and the ventral edge of the septum nasi; it is continued backwards to separate the whole of the lamina transversalis posterior and cupula posterior from the nasal septum.

The postero-lateral edge of the vomer invades the whole length of the posterior paraseptal cartilage.

Due to the presence of an extensive fenestra basalis the middle portion of the nasal capsule has practically no floor. The anterior paraseptal cartilage covers only a relatively small portion of the fenestra antero-medially. As in the posterior paraseptal cartilage it is separated from the nasal septum by a narrow septo-paraseptal fissure. Its posterior tip ends freely and is separated from the posterior paraseptal cartilage by a wide gap. Anteriorly the anterior paraseptal cartilage arises from the ascending medial wall of the lamina transversalis anterior by a long and slender neck. This slender anterior attachment is regarded by STURM (1937) as indicative of the separate origin of the anterior paraseptal cartilage.

The body of the anterior paraseptal cartilage is typically trough-shaped. The vertical medial lamella is well-developed; its ventral edge is strongly recurved laterally, especially in its anterior part, so as to form a ventral and lateral protection for Jacobson's organ. Where the slender neck attaches to the body of the anterior paraseptal cartilage antero-dorsally, a slight roof, or "horizontal lamina" (STURM), is formed. In this region the recurved ventral edge almost meets the "horizontal lamina", but an "outer bar" BROOM is not formed.

Both a cartilago ductus nasopalatini and a cartilago palatina are absent in Setifer.

Anterior to the basal fenestra the solum nasi is formed by the lamina transversalis anterior. This lamina lies at a lower level than the septum nasi so that its medial edge has to ascend in order to fuse with the ventral edge of the septum nasi. The sulcus ventralis nasi so formed is very deep in its posterior part. Laterally the lamina transversalis anterior fuses with the paries nasi to form a complete zona annularis. Anteriorly it is continued into the

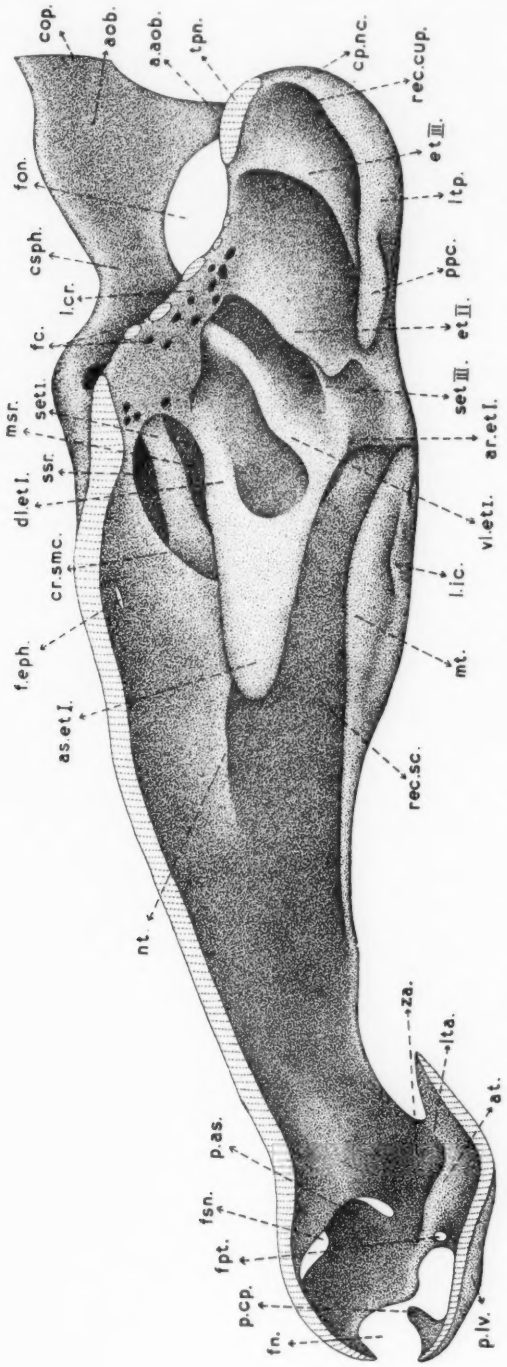

Fig. 65. Medial view reconstruction of the nasal capsule of a 20.4 mm embryo of S. setosus. (The nasal septum has been cut out of the reconstruction.) (× 25).

processus lateralis ventralis which forms the floor of the cupula anterior in front.

Interior of the nasal capsule (fig. 65). A medial view of the paries nasi reveals, especially in the pars posterior and pars intermedia, a series of turbinal cartilages over which the respiratory and olfactory epithelium is spun. These turbinal cartilages are arranged more or less at right angles to the lamina cribrosa and since this lamina is almost horizontally placed, the turbinal cartilages are nearly vertically arranged with a slight backward inclination superiorly. Similarly the recesses enclosed between the turbinal cartilages have a great dorso-ventral depth.

The pars posterior is delimited from the pars intermedia by the attachment of the first primary ethmoturbinal. This ethmoturbinal is by far the largest of the three primary ethmoturbinals and is typically bilaminate in its composition. The larger upper lamella projects horizontally forwards as a blind spur beyond the attachment of its roots and hides from view almost the entire recessus inferior as well as part of the recessus anterior et supraconchalis. The smaller lower lamella is markedly concave antero-superiorly. The turbinal arises from the wall of the nasal capsule by four roots: The posterior root (postero-dorsal in position) arises directly from the ventral surface of the lamina cribrosa. The middle and anterior roots arise, almost in a straight line, from the medial aspect of the paries nasi, producing the sulcus postero-lateralis on its outer surface; the superior root (antero-dorsal in position) arises from the medial aspect of the paries nasi, delimiting the recessus superior (frontalis) from the recessus anterior and inferior (maxillaris).

The second primary ethmoturbinal lies in the pars posterior, behind and parallel to the first primary ethmoturbinal. It is much smaller than the first but is also bilaminate, being composed of a large medial and a smaller lateral lamella; the former lamella completely hides the latter from view. This turbinal springs from the ventral aspect of the lamina cribrosa and the medial aspect of the paries nasi. Enclosed between the first and second primary ethmoturbinals is a deep recess which lodges a small secondary ethmoturbinal at its base (fig. 65).

The third primary ethmoturbinal lies behind and parallel to the second being separated from it by a deep recess which does not lodge any secondary ethmoturbinals. This turbinal is of a simple unilamellar composition and arises from the ventral aspect of the lamina cribrosa and from the medial aspect of the posterior end of the paries nasi. Behind it lies the cupular recess.

The pars intermedia is delimited antero-ventrally, anteriorly and antero-dorsally by the crista semicircularis, the attachment of which produces the sulcus antero-lateralis on the exterior of the paries nasi. The crista semicircularis almost forms a complete semicircle. Its upper limb runs forwards,

VOL.
28
194

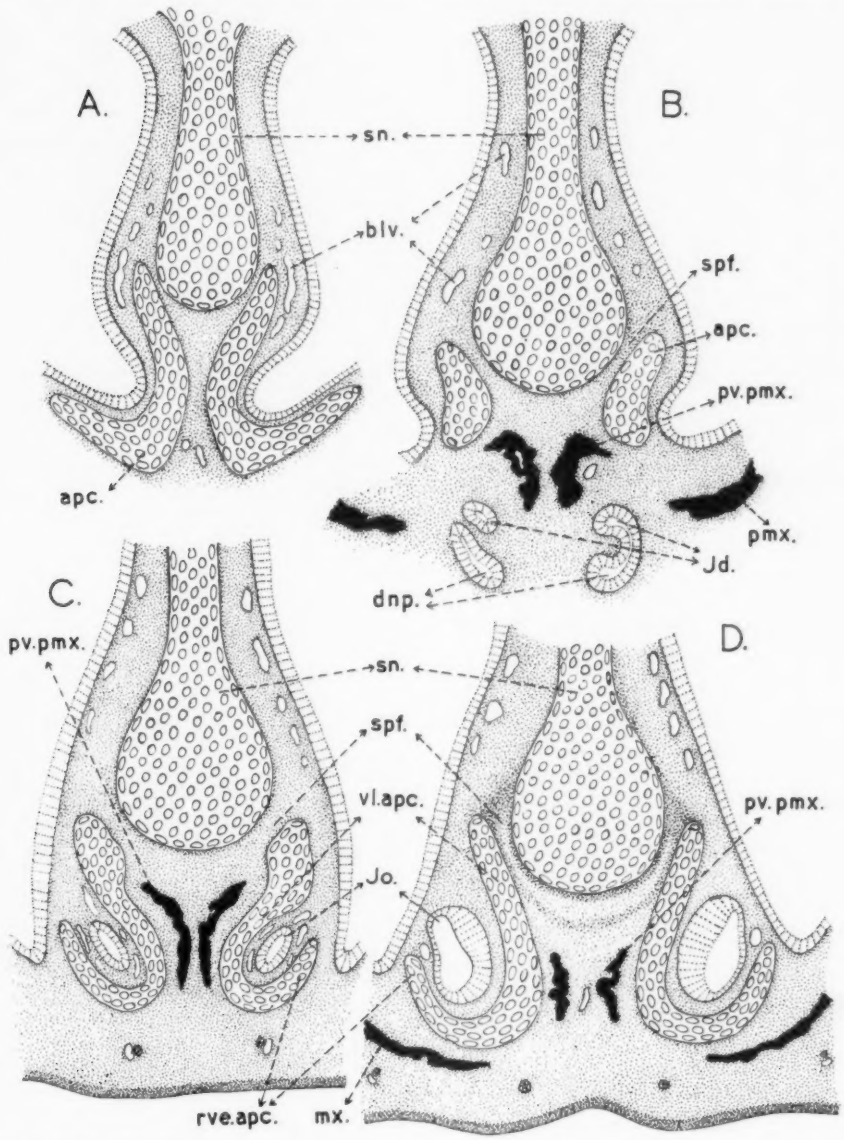

Fig. 66 A—D. Consecutive transverse sections through the nasal septum and anterior paraseptal cartilages of a 20.4 mm embryo of S. setosus (× 60).

laterally and downwards and makes a sharp bend in front of the recessus anterior; the lower limb runs backwards, downwards and medially. The posterior end of the lower limb does not terminate in a free-ending processus uncinatus but gradualy merges into the paries nasi, so that the posterior end

of the recessus supraconchalis communicates freely behind with the recessus inferior.

The attachment of the superior root of the first primary ethmoturbinal divides the pars intermedia into a larger postero-dorsal division, which forms the very deep recessus superior (frontalis), and the smaller antero-ventral division, composed of the recessus anterior and the recessus inferior.

The floor of the recessus superior is formed by the superior root of the first primary ethmoturbinal antero-ventrally and by the middle root of the same ethmoturbinal postero-ventrally. Attached to the base of the recessus superior are the well-defined first and second secondary ethmoturbinals.

Both these secondary ethmoturbinals extend from the superior root of the first primary ethmoturbinal in front, to the cribriform plate behind; they subdivide the recessus superior into three minor secondary recesses. The superior secondary recess lies between the crista semicircularis and the first secondary ethmoturbinal, communicating in front with the recessus anterior. The middle secondary recess (anterior secondary recess, DU TOIT) lies between the first and second secondary ethmoturbinals; the inferior secondary recess lies between the second secondary ethmoturbinal and the middle and superior roots of the first primary ethmoturbinal.

The upper portion of the antero-ventral division of the pars intermedia forms the deep and very far forwards extending recessus anterior which produces the pronounced prominentia anterior externally. This recess which is largely hidden from view by the crista semicircularis, communicates above and behind with the superior secondary recess, postero-ventrally it communicates freely with the recessus inferior (maxillaris). This latter recess communicates in front with the recessus supraconchalis and posteriorly it extends quite a distance as a blind pouch bounded by the paries nasi laterally, the superior root of the first primary ethmoturbinal superiorly, the anterior root of the first primary ethmoturbinal ventrally and the lamellae of the first primary ethmoturbinal medially. The term "recessus glandularis" has been discarded altogether, since the glandula nasalis lateralis lines the whole of the recessus inferior and the major parts of the recessus anterior et supraconchalis.

The pars anterior has a very great antero-posterior length. The maxilloturbinal is well-developed and is restricted to the posterior half of the ventral border of the pars anterior. Posteriorly it ends freely, being separated by a narrow incisure from the ventral edge of the paries nasi. Arising from the posterior division of its ventro-medial edge is a narrow lamina infraconchalis. Anteriorly the maxilloturbinal is separated from the atrioturbinal by a wide incisura maxillo-atrioturbinalis.

The nasoturbinal is poorly developed and does not even extend as far forwards as the maxilloturbinal does. Its attachment to the paries nasi produces a slight sulcus externally, which delimits the prominentia supraconchalis

VOL
28
194

dorsally. Between the nasoturbinal and the maxilloturbinal lies the welldefined recessus supraconchalis which lodges the duct and the greater part of the glandula nasalis lateralis. The atrioturbinal shows the normal relations, being formed as the internal counterpart of the sulcus for the nasolacrimal duct in the region of the zona annularis. It does not communicate behind with the maxilloturbinal.

The septum nasi has the usual shape of a large triangular plate, the base of which is greatly thickened especially in its posterior part between the cupulae posteriores of the nasal capsules. The apex, and therefore also the greatest dorso-ventral depth of the septum, is encountered at the level of the antero-medial ends of the laminae cribrosae. The nasal septum, at this stage, is complete and does not display any deficiencies, either in its anterior or posterior part. Its ventral border is free except for a short distance anteriorly where the laminae transversales anteriores fuse with it. The long antero-superior border is continuously blended with the tectum nasi, and similarly the shorter postero-superior border is joined by laminae cribrosae and the tectum nasi posterius on either side. Posteriorly the nasal septum is continued into the thick cylindrical posterior division of the trabecular plate.

a. *Early development of the nasal capsule:* The nasal capsule is still entirely blastematous in the 9 mm embryo. The nasal septum displays a well-defined autogenous blastem centre, the upper edge of which is in slight blastematous continuity with the tectum and paries nasi. The tectum and paries nasi at this stage is represented by a continuous blastem sheet without any definite concentration in the future partes anterior, intermedia et posterior. The anterior paraseptal displays a local concentration in blastem.

In the 9.3 mm embryo the greater part of the nasal capsule is procartilaginous and the parieto-tectal, paranasal and antorbital centres in the paries and tectum nasi are better defined and more or less clearly delimited from one another by blastem.

The parieto-tectal centre is in slight procartilaginous continuity with the upper edge of the nasal septum in the region of the zona annularis. The anterior tip of the snout is entirely blastematous. The paranasal centre is expanded into the anterior end of the future sphenethmoidal commissure. The antorbital centre is still very small, the greater part of the pars posterior of the nasal capsule being blastematous. The anterior paraseptal is completely blastematous and in slight blastematous continuity with the pars anterior.

In the 9.8 mm embryo conditions are not much different from the previous stage. The nasal capsule is still procartilaginous, the partes anterior et intermedia having lost their separate identity; the pars posterior is still separate; the anterior paraseptal is only defined in blastem and the sphenethmoidal commissure is complete, but only in procartilage.

Even in the 10.5 mm stage conditions are little changed. Except for the

nasal septum the entire nasal capsule is densely procartilaginous. The antorbital centre is fused with the rest of the paries nasi; the anterior paraseptal and the tip of the snout, however, being still only defined in dense blastem. The rest of the early development of the nasal capsule could not be determined due to the lack of embryonic material between the 10.5 and 20.4 mm stages.

b. *Post optimal changes in the nasal capsule:* The post optimal changes in the development of the nasal capsule could not be done in any detail for the same lack of suitable embryonic material. A 47.4 mm embryo, however, shows a few noteworthy changes. As in the 20.4 mm embryo, the nasoturbinal is entirely deficient in its anterior part. The respiratory epithelium of the nose in this region, however, displays a well-defined horizontal ridge without any cartilaginous support, this may imply the future development of the nasoturbinal. This supposition is supported by the fact that a 29.4 mm embryo of the much smaller species of *Echinops telfairi* shows a well-defined nasoturbinal in the region of the zona annularis; this part of the nasoturbinal being discontinuous with its most posterior part. The 47.4 mm embryo of *Setifer setosus* furthermore displays a well-defined third secondary ethmoturbinal at the base of the deep recess between the first and second primary ethmoturbinals. The posterior part of the lamina transversalis posterior is also fused with the lower end of the septum nasi for a short distance.

In the 47.4 mm embryo a small cartilago palatina is present ventro-lateral to the anterior paraseptal cartilage but completely separate from it. A cartilago ductus nasopalatini, however, is still completely absent. Exactly similar conditions were found to prevail in the 29.4 mm stage of *Echinops telfairi*.

The anterior paraseptal in the 47.4 mm embryo of *Setifer setosus* was found to be much similar to that of the 20.4 mm stage. The "outer bar" is still deficient but the vertical lamella in the posterior part of the cartilage is so strongly recurved laterally that it almost forms a complete tunnel for Jacobson's organ. One has good reasons to assume that an "outer bar" (BROOM) may still develop later on, since it is already present in the 29.9 mm embryo of *Echinops telfairi*.

Resorption of cartilage has not advanced very far in the 47.4 mm stage of *Setifer setosus*. The anterior part of the prominentia supraconchalis displays an extensive resorption deficiency roofed over by the maxilla. Similarly the anterior part of the roof of the superior secondary recess of the recessus superior is deficient and roofed over by the frontal.

As far as the ossification of the ethmoid is concerned, three well-defined centres could be distinguished: an unpaired median centre representing the mesethmoid ossification, in the upper part of the nasal septum and the adjoining parts of the laminae cribrosae; two well-defined lateral pleurethmoid ossification centres, each of which involves the entire anteriorly directed spur

VOL
28
194

of the first primary ethmoturbinal with the adjoining anterior ends of the lamellae and anterior root of the turbinal. In addition the posterior paraseptal cartilage and the anterior part of the lamina transversalis posterior are well ossified in conjunction with the vomer at this stage.

The 29.47 mm embryo of *Echinops telfairi* does not show a mesethmoid ossification centre as yet, but in the lateral pleurethmoid region it shows three autogenous centres: one in the anterior spur of the first primary ethmoturbinal; another in the anterior end of the first secondary ethmoturbinal and yet another in the processus uncinatus of the crista semicircularis. In addition, of course, there is the separate ossification centre of the lamina transversalis posterior and posterior paraseptal cartilage in conjunction with the vomer.

C. THE DORSAL STRUCTURE.

The dorso-lateral structures, viz. sphenethmoidal and orbito-parietal commissures and the the parietal plate have already been discussed. The supraoccipital cartilages in Setifer fuse in the mid-dorsal line to form the tectum posterius which forms the postero-dorsal boundary of the foramen magnum. The lateral end of the supraoccipital is fused with the upper posterior end of the exoccipital antero-ventrally, while antero-dorsally it is fused with the parietal plate. A deep sulcus in the postero-lateral aspect of the occipital arch indicates the junctional zone between ex- and supraoccipital cartilages. At this stage of development the greater part of the supraoccipital is already perichondrally ossified.

1. Early development of the supraoccipital cartilage: In the 9 mm embryo the supraoccipital has the form of an extensive blastematous plate, entirely separate from the exoccipital. In the 9.3 mm embryo it is still blastematous, being already fused with the blastem rudiment of its fellow from the opposite side. The 9.8 mm stage displays a small but well-defined chondrification centre in the supraoccipital close to the upper posterior end of the exoccipital. The greater part of the supraoccipital, at this stage, however, is still blastematous. In the 10.5 mm embryo the supraoccipital is extensively chondrified being in cartilaginous continuity with the exoccipital, parietal plate and with its fellow from the opposite side.

2. Post optimal changes in the supraoccipital cartilage: The 20.4 mm embryo displays a fairly extensive perichondral ossification of the supraoccipital cartilages and tectum posterius. It was therefore not possible to determine whether the supraoccipital bone arises from paired lateral centres or from an unpaired median centre.

At this stage of development the supraoccipital ossification is already in slight osseous continuity with the interparietals. During later development this

fusion becomes so intimate that no longer can any line of demarcation be drawn between supraoccipital and interparietal.

The 47.4 mm stage of *Setifer setosus* as well as the 29.4 mm stage of *Echinops telfairi* show a long antero-ventrally directed process of the supra-occipital cartilage, which bridges over the occipito-capsular fissure and overlaps the posterior end of the pars canalicularis of the otic capsule dorso-laterally. This process closely resembles a similar structure described by FAWCETT (1917) in Microtus and again by the same author (1919) in Miniopterus. FAWCETT referred to it as a "processus opercularis" but it seems doubtful whether phylogenetically, it has anything in common with the processus opercularis found in Sorex, Talpa, Suncus and Eremitalpa.

IV. THE MEMBRANE BONES.

The oldest embryonic stage at my disposal, a 47.4 mm embryo, was used for a study of the membrane bones.

VOL 28 194

A. THE PREMAXILLA

presents very little of particular interest. It remains separate from the adjoining bony elements throughout life. The processus extranasalis is very short. The palatine process is also small, forming only the small anterior portion of the hard palate. The processus palatinus medialis, or processus prevomeralis, is strongly developed, being related both to the maxilla and the vomer. It forms the strong medial support for the anterior paraseptal cartilage.

The premaxilla makes its first appearance in ontogeny in the 9.8 mm embryo as a small bony nodule in its future alveolar portion. In the 10.5 mm embryo the processus palatinus medialis was still deficient and in the next stage available (20.4 mm), it was well developed. It was therefore not possible to determine whether or not this process develops from an autogenous centre.

B. THE MAXILLA

is large and consists of the usual parts, viz. a wide frontal process, a well-developed alveolar portion and a wide palatine process which meets its fellow from the opposite side in a median suture, constituting by far the greater part of the hard palate.

The infraorbital foramen is large and pierces the maxilla. Postero-lateral to the infraorbital foramen the maxilla bears a stout zygomatic process directed

backwards and sideways. This process ends freely behind, since a jugal is absent and the zygomatic arch incomplete.

The postero-superior border of the frontal process of the maxilla displays a deep incisure for the transmission of the nasolacrimal duct; the lacrimal bone being absent, the lower border of the frontal converts this incisure into a foramen.

The maxilla first appears in the 9.8 mm embryo. It arises from two centres: one in the future zygomatic process and another at about the junction of the future frontal and alveolar portions; these two centres are completely fused in the 20.4 mm embryo.

The presence of a separate ossification centre for the zygomatic process of the maxilla is important because it may mean that this process actually represents the missing jugal of the Centetidae. Additional developmental data for other members of the Centetidae is necessary however, before any definite statements can be made. LEIMGRUBER (1939) reported a separate centre for *Tenrec ecaudatus*.

VOL. 28 1947

C. THE JUGAL

is commonly regarded as absent in the Centetidae and no separate jugal could be found in Setifer, unless the zygomatic process of the maxilla is regarded as the rudiment of the jugal which became secondarily fused with the maxilla. (See development of maxilla.)

D. THE LACRIMAL BONE

is absent in the 47.4 mm embryo; neither could it be found in the younger stages, the oldest of which measured only 20.4 mm. This, however, is not surprising because the lacrimal usually appears very late in ontogeny. Its absence in the 47.4 mm embryo, therefore, may not necessarily mean that it is entirely absent in *Setifer setosus*, it may not have developed as yet or it may have developed after the 20.4 mm stage and have fused again with the maxilla (or frontal) before the 47.4 mm stage was reached.

This latter possibility is supported by the condition prevalent in *Echinops telfairi* MARTIN, of which a 29.4 mm embryo was sectioned. This latter species is much smaller than *Setifer setosus*, consequently the chondrocranium and membrane bones in the 29.4 mm embryo were at least as well, if not better developed than in the 47.4 mm embryo of *Setifer setosus*.

The 29.4 mm embryo of *Echinops telfairi* shows a well-defined and separate lacrimal bone on the prominentia inferior of the nasal capsule. It is not pierced by the lacrimal canal, but its anterior part, which lies under cover of the maxilla, is trough-shaped and lodges the nasolacrimal duct. Its posterior

part lies wedged between the frontal and alveolar portions of the maxilla, so that the lacrimal bone forms the posterior delimitation of the lacrimal canal.

The lacrimal has been reported as absent only in Monotremes, Manis and Pinnipedia and as STADTMÜLLER (1936) maintains, this absence is only apparent, since in most cases it is regarded as fused either with the frontal or with the maxilla.

E. THE VOMER

is trough-shaped. Being unpaired, it lodges the lower edge of the nasal septum and extends from between the anterior ends of the anterior paraseptal cartilages to a point behind the cupulae posteriores of the nasal capsules. The anterior half of the vomer forms a very deep trough with fairly thin walls but a thick, in parts even pneumatic, base. This part of the vomer is intimately related with the processus prevomerales of the premaxillae and with the palatine processes of the maxillae.

In its posterior half the vomer assumes the shape of a very shallow trough, its extreme posterior part being merely a horizontal plate below the nasal septum. Where it lies between the posterior paraseptal cartilages and laminae transversales posteriores, the vomer, at this stage, displays extensive horizontally-placed wings, which are formed by the ossified posterior paraseptal cartilages and medial edges of the posterior transverse laminae. The extreme posterior end of the vomer is related to the vertical laminae of the palatines, the orbitosphenoids and the pterygoids.

Because of the lack of suitable embryonic stages the earliest development of the vomer could not be determined. In the 10.5 mm embryo it is still absent and in the 20.4 mm stage it is a strongly developed trough-shaped bone, which has even commenced its invasion of the posterior paraseptal cartilages.

F. THE PALATINE

is of moderate size but presents little of particular interest. Its horizontal lamina forms the posterior part of the hard palate and thus the anterior boundary of the apertura nasalis interna. The vertical lamina is trough-shaped and is intimately related to the orbitosphenoid, alisphenoid, vomer and pterygoid.

Its earliest development could not be determined. It is still absent in the 10.5 mm embryo and already well-developed in the 20.4 mm stage.

G. THE PTERYGOID

is a thick, well-defined bone, intimately related to the palatine, vomer, alisphenoid and basisphenoid. It does not fuse either with the vomer or with the

VOL. 28 194

palatine, but its posterior end is inseparably fused with the alisphenoid and basisphenoid. The hamulus is also well-developed, and at this stage still contains a large nodule of the pterygoid cartilage in its posterior extremity.

Its earliest development could not be determined, since it was absent in the 10.5 mm embryo but well-developed in the 20.4 mm stage. In the latter stage the posterior end of the pterygoid is already fused with the basisphenoid but is still completely separate from the ala temporalis.

H. THE NASAL

present nothing of particular interest. It extends backwards about as far as the middle of the nasal capsule and ends by forming an intimate suture with the frontal. It is furthermore related to the premaxilla and maxilla, and at this stage of development is completely fused with its fellow from the opposite side in the mid-dorsal line.

The stage at which it first appears could not be determined, but in the 20.4 mm embryo the nasal i already extensively ossified and its posterior end is fused with its fellow from the opposite side.

I. THE FRONTAL

is a fairly extensive bony plate, being related to the nasal, maxilla, palatine, orbitosphenoid and pterygoid. It is strongly pneumatic, especially along its dorso-lateral aspect and displays an extensive frontal sinus. It was observed for the first time in the 9.8 mm embryo, dorso-lateral to the prominentia superior of the nasal capsule and lateral to the sphenethmoidal commissure.

J. THE PARIETAL

is an extensive bony plate but not as thick and pneumatic as the frontal. It is related to the frontal, orbito- and alisphenoids, squamosal and interparietal.

It was observed for the first time in the 20.4 mm embryo as an extensive plate lateral to the orbito-parietal commissure and parietal plate.

K. THE SQUAMOSAL

is of moderate size and of a relatively simple composition. It is related to the alisphenoid and parietal. The glenoid cavity has the form of a simple but fairly extensive horizontal shelf. No post-glenoid process is present but the part of the squamosal that projects backwards from the glenoid cavity bears a conspicuous horizontally situated ridge. No zygomatic process is present.

Its earliest development could not be determined because of the lack of suitable embryonic material. It was first observed in the 20.4 mm embryo where the squamosal is fairly well developed, especially its glenoid portion, which already bears a long backwardly directed spur at this stage.

L. THE INTERPARIETAL

is an extensive plate which at this stage is inseparably fused with the supra-occipital but is still separated from the parietals by a wide fontanella.

In the 20.4 mm embryo, where it was observed for the first time, the interparietal was still almost completely divided into two lateral halves. Each of these, a well-fenestrated plate, was lying supero-medial to the occipito-parietal commissure. Posteriorly it was found to be in slight continuity with the supraoccipital ossification and with its fellow from the opposite side.

VOL
28
194

M. THE TYMPANIC (ECTOTYMPANIC)

still displays the primitive C-shape, the deficiency facing slightly upwards and laterally. The short antero-lateral limb is closely related to the ventral aspect of the posterior extremity of Meckel's cartilage, the prearticular intervening. Due to the lack of older embryonic stages, it was not possible to determine the utimate fate of the ectotympanic which, however, is believed to retain its primitive form throughout life, as is the case in Monotremes, Didelphidae, Chiroptera, Xenarthra as well as in many other Insectivores, Orycteropus, Sirenia, Lemuridae and Chiromyidae.

In Setifer it was observed for the first time in the 20.4 mm embryo as an extensive rod with a long medial and a short anterior limb. In the younger stage investigated, a 10.5 mm embryo, it was entirely absent.

N. THE PREARTICULAR (GONIAL)

is a short, trough-shaped membrane bone which invests the ventral aspect of the posterior extremity of Meckel's cartilage and ends behind by invading the neck of the malleus. The medial wall of the trough displays a small foramen for the transmission of the chorda tympani nerve.

It was first observed in the 20.4 mm embryo where it appeared as a minute splint of bone lying ventral to the posterior end of Meckel's cartilage. At this stage it does not invade the neck of the malleus and neither does it display a foramen for the chorda tympani nerve.

V. SUMMARY.

The following points in the development of the chondrocranium and early osteocranium of Setifer are noteworthy:

a. *The central stem.*

1. The central stem is almost straight as in all typical Insectivores.
2. The dorsum sellae is inconspicuous and the fossa hypophyseos illdefined.
3. The basicochlear fissure is present and undivided.
4. The anterior and posterior basicochlear commissures are both deficient.
5. The chorda dorsalis is completely resorbed at the optimal stage of chondrification of the chondrocranium.
6. The fenestra hypophyseos is obliterated very early in the development of the lamina hypophyseos.
7. The alicochlear commissures are present and well-developed.
8. The planum basale, in its early development, clearly illustrates the presence of paired parachordal cartilages separated by an extensive fenestra basicranialis posterior.
9. The notochord remains dorsal to the planum basale until it is resorbed again.
10. No paired "polar elements" could be identified in the chondrification of the lamina hypophyseos.
11. The processus alaris, as well as the alicochlear commissure chondrify in continuity with the lamina hypophyseos.
12. The pars trabecularis of the central stem remains clearly demarcated from the lamina hypophyseos until relatively late in their development.
13. The central stem displays three unpaired ossification centres: basioccipital, basisphenoid and mesethmoid. The presphenoid arises from the orbitosphenoids.
14. The adult basicranial axis, thus, is composed of four elements.
15. The basisphenoid bears a pair of conspicuous tympanic wings.

b. *Exoccipital cartilages.*

1. The exoccipital cartilages are massive and bear a pair of well-defined occipital condyles.
2. A single pair of hypoglossal foramina is present.
3. The processus paracondyloideus is massive.
4. The recessus supra-alaris is wide.
5. The lamina alaris is in weak synchondrotic continuity with the pars canalicularis of the auditory capsule.
6. The superior and inferior occipito-capsular fissures are confluent.

VOL. 28 1947

7. The exoccipital cartilage seems to chondrify in continuity with the planum basale and not from a separate centre.
8. The exoccipital bone ossifies from a single autogenous centre and forms the major part of the occipital condyle.

c. *Auditory capsule.*

1. The posterior occipito-capsular commissure is deficient as well as the anterior and posterior basicochlear commissures.
2. The parietal plate is very large and both the orbito-parietal and occipito-parietal commissures are well defined.
3. An opercular process (FISCHER) is absent.
4. The tegmen tympani is absent.
5. The crista parotica is massive.
6. The subarcuata fossae in the pars canalicularis of the auditory capsule are rather ill-defined.
7. A primary suprafacial (medial pre-facial) commissure, as well as a secondary suprafacial (lateral pre-facial) commissure are present.
8. The cochlear segment of the auditory capsule displays a well-defined sulcus septalis and also another sulcus for the internal carotid artery and deep petrosal nerve.
9. A foramen singulare is present.
10. The foramen endolymphaticum is situated relatively far back on the prominentia cruris communis.
11. The processus recessus and associated structures display rather primitive relations.
12. The auditory capsule chondrifies from two main centres; one in the pars cochlearis and the other in the pars canalicularis.
13. The parietal plate seems to arise from an autogenous centre.
14. The primary suprafacial commissure appears very long before the secondary suprafacial commissure.
15. The rudimentary processus recessus makes its appearance relatively early in ontogeny.
16. The auditory capsule ossifies from three main centres.
17. No rostral or caudal entotympanics or rostral and caudal petrosal tympanic plates could be distinguished.

d. *Ala temporalis.*

1. The ala temporalis is a fairly extensive plate, inclined dorsally at an angle of $\pm$ 40°.
2. A wellmarked incisura ovalis is present.
3. A foramen alisphenoidale is isolated.
4. The processus pterygoideus is present, but is short and wide.

VOL
28
194

5. Both the processus alaris and alicochlear commissure are intact.
6. The ala temporalis chondrifies from an autogenous centre, but no separate centre for the pterygoid process could be distinguished.
7. The alisphenoid ossifies from a separate centre and the pterygoid fuses with it.

e. *Ala orbitalis.*

1. The ala orbitalis is rather slender and rodlike.
2. Both the sphenethmoidal and orbito-parietal commissure are intact.
3. The pre- and post-optic roots of the ala orbitalis are slender and join the pars trabecularis by means of a short common stem.
4. The ala hypochiasmata is well-defined and forms a shelf beneath the small and slanting optic foramen.
5. The ala orbitalis chondrifies from an autogenous centre, but a separate centre for the ala hypochiasmata could not be distinguished.
6. The development of the preoptic root of the ala orbitalis is always well in advance of the postoptic root.
7. Whether the orbitosphenoid ossifies from a single centre or from two centres could not be determined, but the two orbitosphenoids do invade the central stem to form the adult presphenoid of the basicranial axis.

f. *Nasal capsule.*

1. The nasal capsule is long and pear-shaped; about one third being subcerebral and the rest precerebral in position.
2. The crista galli is rather ill-defined.
3. The tectum nasi posterius is almost horizontal in position.
4. The laminae cribrosae are well fenestrated.
5. The epiphanial foramina are present.
6. The maxilloturbinal bears a small lamina infraconchalis on its ventrolateral surface.
7. The zona annularis is complete.
8. A small foramen pretransversale is isolated for the transmission of the nasolacrimal duct.
9. The cupulae anteriores of the nasal capsule are well-defined and separated by the cavum internasale.
10. The fenestra superior nasi is present.
11. Both a processus cupularis and a processus alaris superior are present.
12. The lamina transversalis posterior and the posterior paraseptal cartilage are both present and separated from the septum by a septo-paraseptal fissure.
13. The anterior paraseptal cartilage is well defined and of the more specialized variety.

VOL. 28 1947

14. An "outer bar" could not be demonstrated in *Setifer setosus* but it was found to be present in *Echinops telfairi.*
15. The turbinal cartilages in the pars posterior and pars intermedia of the nasal capsule are almost vertically placed.
16. Both the first and second primary ethmoturbinals are of a bilaminate composition.
17. Three secondary ethmoturbinals were found in the latest embryonic stages investigated.
18. The crista semicircularis does not bear a free-pointed processus uncinatus.
19. The nasoturbinal is poorly developed in *Setifer setosus but* is much better defined in *Echinops telfairi.*
20. The atrioturbinal does not communicate with the maxilloturbinal.
21. The nasal septum does not display any deficiencies.
22. The early development of the nasal capsule displays well-defined blastematous antorbital, paranasal and parieto-tectal centres.
23. The anterior paraseptal also displays a well-defined autogenous blastem centre.
24. A small cartilago palatina is present in the oldest embryonic stage investigated, but a cartilago ductus nasopalatini could not be demonstrated.
25. The main pleurethmoidal ossification centre is situated in the anterior end of the first primary ethmoturbinal.

g. *Supraoccipital cartilage*

1. The tectum posterius chondrifies from bilateral supraoccipital centres.
2. It could not be determined whether or not the supraoccipital bone arises from paired centres.
3. The interparietals fuse with the supraoccipital ossification very early.
4. In the oldest stages investigated the supraoccipital cartilage, both in *Setifer setosus* and in *Echinops telfairi,* bears a long antero-ventrally directed wing as in the Golden Mole (Author).

h. *Membrane bones.*

1. The premaxilla displays small extra nasal and palatine processes, but its processus prevomeralis is well-defined.
2. No separate ossification centre for the processus prevomeralis could be detected.
3. The short zygomatic process of the maxilla displays an autogenous ossification centre which strongly suggests that it represents the rudimentary jugal.
4. The zygomatic arch is most incomplete.
5. A separate lacrimal bone could not be demonstrated in *Setifer setosus,* but it was found to be present in *Echinops* telfairi.

VOL.
28
194

6. The vomer extensively invades the lamina transversalis posterior and the posterior paraseptal cartilage.
7. The pterygoid displays a well-defined pterygoid cartilage and at an early stage of development it fuses with the basisphenoid. Later on it also fuses with the alisphenoid.
8. The palatine, nasal, frontal and parietal present nothing of particular interest.
9. The squamosal lacks a zygomatic process.
10. Paired interparietal ossification centres could be fairly well distinguished.
11. The tympanic bone presents the usual C-shape. Neither its earliest development nor its ultimate fate could be determined.
12. The prearticular displays a small foramen for the transmission of the chorda tympani nerve.

OL.
28
947

PART V. DISCUSSION OF THE RESULTS OBTAINED IN PREVIOUS PARTS OF THIS PAPER.

I. INTRODUCTION.

As stated in preceding pages, this research on "Insectivore" embryonic material has been undertaken to contribute to a better knowledge of the embryology and comparative anatomy of this much disputed group, lying, as it does, on the "cross-roads" of Mammalian phylogeny.

Investigation into the material at our disposal (Elephantulus, Suncus, Eremitalpa and Setifer), has involved certain problems concerning the morphology and taxonomy of the group. These will now be discussed.

II. SPECIFIC MORPHOLOGICAL CONSIDERATIONS.

1. The prechordal region of the central stem: As GOODRICH (1930) rightly remarks, the prechordal region of the central stem is somewhat difficult to interpret. As is commonly the case in Mammals, the prechordal portion of the central stem in the "Insectivores" investigated, develops in two regions. The most anterior of this, i.e. the pars interorbitonasalis (FAWCETT), anterior trabecular element (GOODRICH) or trabecular plate (STADTMÜLLER) arises as an unpaired median element, which fuses with the rest of the central stem at a very early stage in Suncus—while still entirely

blastematous. In Elephantulus, Eremitalpa and Setifer, however, it retains its separate identity for a longer period, and in the latter two, separate chondrification centres can be clearly distinguished. This part of the central stem is commonly believed to represent the fused anterior parts of the two primitive trabeculae cranii.

The difficulty, however, lies in the interpretation of that part of the central stem interposed between the trabecular plate in front and the parachordal (or basal) plate behind. This region of the Mammalian central stem, called the lamina hypophyseos, (pars trabecularis of FAWCETT and lamina polaris of other authors) is commonly regarded as arising in placental Mammals from paired elements lateral or postero-lateral to the hypophysis and medial to the internal carotid arteries. The lamina is completed by a "later" backgrowth of cartilage round the lateral aspects of the internal carotid arteries gaining secondary attachment to the front of the cochlear capsules. GOODRICH 1930, DE BEER 1929 and 1937 and STADTMÜLLER 1936 give exhaustive accounts of the various opinions expressed as to the possible homologies of the elements concerned, and to them the reader is referred for further particulars.

In the specimens investigated these problematic elements, lying medial to the internal carotid arteries, were never clearly defined, not even in blastem. Only in Suncus could definite paired blastem and chondrification centres for these elements be distinguished.

In the following respects, however, the development of the lamina hypophyseos was found to be identical in these forms: 1. The central part of the lamina hypophyseos, whether displaying paired centres or not, was found to fuse with the basal plate behind earlier than with the trabecular plate in front. 2. Chondrification was found to spread from this central part of the lamina hypophyseos, first into the processus alares and then backwards into the alicochlear commissures, lateral to the internal carotid arteries, if, indeed, these commissures did develop at all. (They are absent in Eremitalpa.)

The central part of the lamina hypophyseos is regarded to be of secondary origin by DE BEER. He compares it to the taenia intertrabecularis of Chelonia and therefore suggests the term "hypophyseal cartilages" for the elements constituting it, in preference to the term "polar cartilages" applied by NOORDENBOS, who compares them to the "polar cartilages" of VAN WYHE (detached posterior ends of trabeculae cranii).

The view that this central part of the lamina hypophyseos is composed of the posterior ends of the trabeculae (LEVI, FAWCETT and others) is thus strongly opposed by DE BEER and also by GOODRICH, who see in the alicochlear commissures the ontogenetically delayed posterior ends of the trabeculae, or the true "polar cartilages" of VAN WYHE.

The development of the lamina hypophyseos in "Insectivores", and for that matter in all Mammals, however, seems to suggest that the posterior ends

VOL. 28 194

of the trabeculae have come to surround the internal carotid arteries—these being in a process of cutting through the bases of the trabeculae cranii or "polar cartilages", as maintained by GAUPP. This view is supported by the fact that the basitrabecular process (processus alaris) chondrifies from the medially placed element and that the alicochlear commissure, in turn, chondrifies from the processus alaris. Furthermore, one would expect the phylogenetically older element to be recapitulated first in ontogeny and there is no doubt that the alicochlear commissure, if present, always makes its appearance relatively late in ontogeny as compared to the median element. To regard the alicochlear commissure as a secondarily acquired structure, however, seems to be of no avail, much rather do we regard it as a rudiment of the postero-lateral end of the trabecula in a state of rapid regression. The reason for this progressive specialization in the hypophysial region—lateral migration of the internal carotid arteries and medial migration of the posterior ends of the trabeculae cranii—is probably to be found in the progressive narrowing of the anterior end of the parachordal (basal) plate, to which the trabeculae gain their primary attachment.

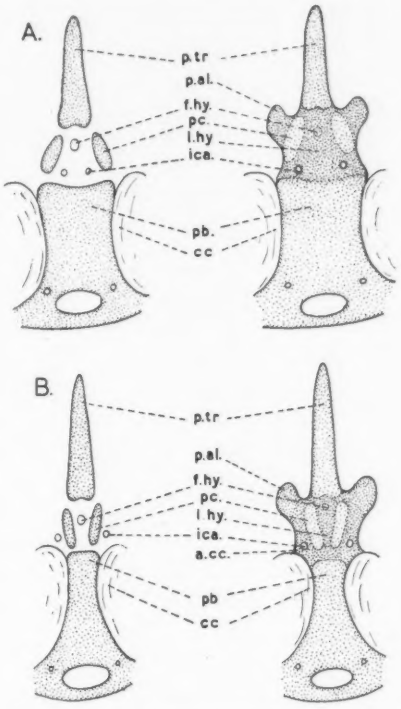

Fig. 67. Diagramatic representation of the formation of the lamina hypophyseos in Mammals: A. Monotremes. B. Placental Mammals. *a.cc.* alicochlear commissure; *cc.* cochlear capsule; *f.hy.* fenestra hypophyseos; *ica.* internal carotid artery; *l.hy.* lamina hypophyseos; *p.al.* processus alaris; *pb.* planum basale; *pc.* polar cartilage; *p.tr.* pars trabecularis of central stem.

In Monotremes the anterior end of the parachordal plate is wide and the cochlear capsules far apart. In them the primitive Vertebrate condition in which the trabeculae, although lateral to the internal carotids, still attach to the parachordal plate, is found to prevail. In Marsupials an intermediate stage is encountered which leads to the ultimate condition prevalent in most placental Mammals, where the medially converging cochlear capsules encroach upon the anterior end of the parachordal plate, suppressing it to a marked degree. The posterior ends of the trabeculae cranii thus, would necessarily have attached secondarily to the cochlear capsules (as the regressing alicochlear commissures do) had it not been for their medial migration.

The internal carotid arteries, to prevent compression medially between the

posterior ends of the trabeculae cranii, in front of the medially and anteriorly expanding cochlear capsules show a tendency to escape laterally by cutting through the posterior ends of the trabeculae and slipping round the antero-lateral margins of the cochlear capsules (fig. 67).

2. Chondrification and ossification of the auditory capsule: As is usually the case in Mammals, the auditory capsule in the material investigated was found to chondrify from two main centres: one in its future pars canalicularis and another in the future pars cochlearis. These two centres remain more or less distinct for some time before becoming interconnected via the pars vestibularis. It has further been determined that the pars cochlearis chondrifies in situ and does not arise from the anterior part of the planum basale (on which it encroaches) as was maintained by GAUPP (1900).

This view of GAUPP, however, has never gained any wide support and was subsequently abandoned as conditions in Cetacea, Halicore and Felis became known, where a well-defined (or rudimentary) lamina supracochlearis overlies the cochlear capsule and gives attachment to the alicochlear commissure. (See DE BEER 1937.)

That the attachment of the alicochlear commissure to the cochlear capsule in most Mammals is of secondary nature is furthermore suggested by the progressive reduction of this structure in Mammals and the simultaneous stronger development of the median portion of the lamina hypophyseos which still retains its primary attachment to the planum basale of the central stem.

The ossification of the auditory capsule in the Chrysochloridae, Menotyphla and Insectivora was found to emanate from three main ossification centres: one in the extreme antero-lateral part of the pars vestibularis, another in the extreme postero-ventral part of the pars cochlearis and yet another in the pars canalicularis. These centres, however, are not very well circumscribed and their exact position is also subjected to slight variations in differant groups.

Apart from these main centres several other minor or less constant centres may also make their appearance e.g. in the tympanohyale, opercular process (when present) and anterior end of the cochlear capsule.

ANDRES (1924) described as many as ten to twelve ossification centres in the auditory capsule of the pig. STADTMÜLLER (1936) however, pointed out that these centres can be divided into two main groups: An anterior inner group of centres which he regards as the possible homologue of the pro-otic of lower Vertebrates, and posterior outer group of centres which he regards as possibly homologous with the epi-otic and opisth-otic of lower forms.

3. The "opercular" process and "tabular": The presence of an opercular process has first been reported by FISCHER (1901) in Talpa. It has subsequently been described in Sorex (DE BEER 1929), Suncus and Eremitalpa (Author).

In all these forms mentioned, the opercular process has the form of a fairly broad, sagittally placed plate which is fused below with the otic capsule and the anterior, upper and posterior edges of which are free. It lies lateral to the capsulo-parietal commissure and the anterior end of the superior occipito-capsular fissure, thus supplying a ventro-lateral wall to the deep sulcus lodging the lateral jugular vein.

From its development in Suncus and Eremitalpa it has been established beyond any doubt that the opercular process arises in situ as an outgrowth from the otic capsule which, as is the case in Eremitalpa, may appear very late in ontogeny. This fact probably accounts for its absence having been reported in so many Mammalian chondrocrania investigated. It appears to be devoid of any phylogenetic significance, having developed, as it seems, to afford protection for the lateral jugular vein.

Apart from the opercular process mentioned, however, FAWCETT described an antero-ventrally directed prolongation of the supraoccipital in Microtus (1917), Poecilophoca (1918) and Miniopterus (1919). A somewhat similar process has been reported present in Suncus and Eremitalpa (Author). This process was found to arise ontogenetically in continuity with the supra-occipital and there appears to be very little justification for regarding it as homologous with the opercular process of FISCHER, as indeed DE BEER and FAWCETT suggested. Furthermore the simultaneous presence of both processes in Suncus and in Eremitalpa strongly contradicts this view.

More-over, the opercular process of FAWCETT does not seem to be a definite anatomical entity, being present in most Mammals to a greater or lesser degree. It merely represents an anteriorly or antero-ventrally directed expansion of the supra- (and ex-) occipital cartilage(s), which, because of its very poor development (or even entire absence) in some forms, failed to arouse comment. That this process is of great significance is suggested by the condition prevalent in the Golden Mole. As previously stated it is of enormous size in the Golden Mole, being directed more forwards than downwards.

Of importance, however, is the appearance of an autogenous ossification centre in the postero-ventral part of this process during later embryonic development. This ossification which spreads forwards, upwards and downwards proves to be the "tabular" found in the otic region of the juvenile mole.

The presence of this element in the skull of the Golden Mole has first been reported by LECHE (1907—quoted after WEBER 1927), who referred to it as a pteroticum. BROOM (1916), describing this bone in the skull of a juvenile *Chrysochloris asiatica*, expressed his views on its homology as follows: "Whatever be the nature of this bone, it quite certainly, as will be seen later, is not formed from any part of the ear capsule, and as it certainly occupies the exact position of the tabular in Therapsid and other reptiles, it seems well to apply this name to it. As a large tabular occurs in Cynodonts we may infer that the

early Mammals still retained it, and possibly Chrysochloris and its ancestors have never lost this ancestral character which all other known Mammals have lost" (pp. 451—452).

BROOM, as most other investigators, regarded this element as being a membrane bone and therefore the homology with the reptilian tabular seemed very likely. As the development of this element in Eremitalpa proves, however, it is not a membrane bone but a cartilage bone arising in the expanded supraoccipital cartilage. Actually WINGE (1923) (quoted after WEBER), regarded it as "einen abgesprengten Teil des Supraoccipitale, aus Verbreiterung des Hinterschädels entstanden", and this, for the time being, seems to be the most satisfactory evaluation of its significance.

Whether in Phoca, in which the presence of a tabular has first been reported, it is also preformed in the supraoccipital cartilage has not yet been ascertained.

4. Ossification of the central stem (basi-cranial axis): In text-books the central stem of the chondrocranium is always described as being typically composed of four elements, viz: a basioccipital arising in the basal plate in front of the foramen magnum; a basisphenoid arising in the lamina hypophyseos; a presphenoid arising in the pars trabecularis medial to the optic foramina and finally a mesethmoid which arises in the region of the crista galli of the intranarial portion of the pars trabecularis.

As BROOM (1926 and 1927), has pointed out, however, this contention is erroneous because in Marsupials and Artiodactyls there are never more than three elements participating in the formation of the basicranial axis. This condition, according to BROOM, moreover, represents the primitive Mammalian condition because it corresponds with the condition prevalent in Therapsid reptiles from which the Mammals have sprung. He therefore concludes, on the basis of homology with the Therapsida, that the three elements present in the Marsupials and Artiodactyls are the basioccipital, basisphenoid and presphenoid; the mesethmoid, if present in Mammals, representing a neomorph.

On this basis BROOM (1927) divides the Eutheria into two groups, the more primitive of which he names the Palaeotherida (with only three elements in the basicranial axis), and the more specialised group the Neotherida (with four elements in the basicranial axis). Both the Marsupials and the Monotremes lack the fourth element.

That BROOM has touched here on a problem of great morphological significance is beyond any dispute. It is, however, most unfortunate that the two problematic elements concerned—the presphenoid and mesethmoid—make their appearance so late in intrauterine development or in early post-natal life, that their development has not been subjected in the past to the thorough microscopical investigation they seem to call for.

Amongst the "Insectivores" investigated by the author (Suncus, Elephantulus, Setifer and Eremitalpa) were members of both BROOM's Palaeotherida

and Neotherida, and fortunately three of these (Suncus, Elephantulus and Setifer) belong to the more specialised Neotherida, possessing four elements in the basicranial axis. Of all these, fairly late embryonic stages or even juvenile forms were available, and although the development of the problematic elements concerned could not be exhaustively studied, the data available, never the less leave very little doubt as to the exact composition of the basicranial axis in these forms. From these, and from the information gained from BROOM's accounts (1926 and 1927), one can draw fairly reliable conclusions.

In the Chrysochloridae (as represented by Eremitalpa) only three elements participate in the formation of the basicranial axis, thus confining them to BROOM's Palaeotherida together with the Xenarthra, Artiodactyla, Perissodactyla, Pholidota and Cetacea. Of the three elements concerned, the basioccipital is of undisputed identity and needs no further mentioning. Similarly, the basisphenoid is of sure homology, but it needs further consideration because this element extends forwards by continuous ossification into the presphenoidal region where it definitely separates the most medially extending ends of the orbitosphenoids, thereby eliminating the possibility for these elements to enter into the formation of the adult basicranial axis. The orbitosphenoids, having been eliminated, two possibilities theoretically remain for the ossification of the remainder of the pars trabecularis: 1. It may ossify from a single centre—presphenoid or mesethmoid. 2. Both these centres may appear so that the basicranial axis will, in that case, be composed of four elements.

This final step in the ossification of the central stem could not be determined in Eremitalpa due to the lack of suitable material. BROOM (1927) however, gives the answer in *Chrysochloris asiatica,* where it is demonstrated beyond any doubt that this part of the central stem ossifies from a single centre, which he prefers to call the presphenoid.

This centre is situated relatively far forwards, being at least as far forward as the most posterior tip of the nasal septum. In position it corresponds exactly with the mesethmoid of higher Mammals and with the anterior basicranial element found in Therapsid Reptiles (Dicynodon BROOM 1926). There is no reason to doubt that this condition prevails in all the Chrysochloridae.

A very interesting condition of the central stem is encountered in the Marsupials. PARKER (1885), without going into any details, mentions that: "The orbitosphenoids do not form the presphenoid by meeting together below, but the presphenoid is as independent as the basisphenoid" (p. 271). BROOM (1926) throws more light on the Marsupial condition. He mentions that in Trichosurus a definite autogenous, *but unpaired* ossification centre makes its appearance in the central stem between the two orbitosphenoid.

This centre, after having been reinforced by the medially extending orbitosphenoid ossifications, expands forwards and culminates in the complete

ossification of the mesethmoid region. BROOM finds good reason to assume that a similar condition obtains in all Marsupials. Moreover, he relates an almost identical condition for the Artiodactyla, with the only exception that the orbitosphenoid contributions to the "presphenoid element" are more extensive than was the case in the Marsupials. In none of the other Mammals showing only three elements in the basicranial axis, and therefore belonging to BROOM's (1937) Palaeotherida, has the development of the anterior "presphenoidal" element been studied sufficiently well to enable one to be absolutely sure as to its composition.

Three possibilities, however, seem to exist: 1. It may arise solely, as in the case of the Golden Mole, from a single unpaired ossification centre in the pars trabecularis of the central stem. 2. It may, as in the case of Trichosurus, be a complex element formed from an unpaired median centre which has been reinforced laterally by the orbitosphenoids. 3. It may be formed merely from the medially extending orbitosphenoid ossifications. (This condition is purely hypothetical and has not been reported to exist in any Mammal).

From the account given above it is obvious that BROOM's Palaeotherida does not constitute a homogeneous group. At least two, if not three elements enter into the formation of the most anterior basicranial element found in this group.

There can be little doubt that in the Chrysochloridae the condition of the basicranial axis resembles that of Therapsid Reptiles strikingly. There seems to be very little reason why the unpaired presphenoidal ossification centre described by BROOM for Trichosurus should not be regarded as identical with the ossification centre giving rise to the "anterior element" in Golden Moles. The centre in the Golden Mole is situated slightly further forwards than that of the Marsupial, but this does not seem to exclude the possibility of strict homology, because, unlike the basisphenoid and basioccipital, these ossification centres do not arise in a part of the central stem of the chondrocranium which develops ontogenetically from separate centres—the pars trabecularis (planum interorbitonasalis) being a homogeneous entity.

The Marsupial basicranial axis could therefore be regarded as strictly identical with that of the Golden Moles had it not been for the secondary invasion of the anterior element by the orbitosphenoids, thus rendering this element of complex nature. It cannot as yet be determined to what extent the Marsupial or Golden Mole conditions prevail in the other members of BROOM's Palaeotherida.

Coming to the members of BROOM's Neotherida we have to account for an additional element which enters into the formation of the basicranial axis. Theoretically, this new element, being the mesethmoid, has to form the most anterior tip of the basicranial axis. This, however, is not the case. The most anterior part of the basicranial axis is still formed by the unpaired anterior ossification centre found in the Palaeotherida, but shifted relatively far for-

wards as in the Golden Moles, i.e. the presphenoidal centre of BROOM. The new element is introduced between this centre in front and the basisphenoid behind; the only difference being that in the Neotherida the basisphenoid ossification remains restricted to the lamina hypophyseos of the central stem, while the anterior ossification centre involves exclusively the intranarial portion of the pars trabecularis and the laminae cribrosae, leaving the hindermost part of the pars trabecularis to the newly introduced element.

The question arises as to the nature of this fourth element which comes to be interposed between the basisphenoid behind, and the unpaired ossification centre (presphenoid or mesethmoid) in front. It definitely occupies the "classical" position of the presphenoid and always arises, if not directly from the orbitosphenoids, then from paired centres, one in the medial margin of each optic foramen. It is important to note that it never (from our present knowledge) arises from an unpaired median centre; so that a basicranial axis displaying four elements, arising in series from unpaired median centres of ossification is unknown amongst Mammals, and for that matter, amongst all Vertebrates.

The development of this fourth element in Suncus, Setifer and Elephantulus leaves very little doubt, if any, as to its true nature and significance.

In Suncus, no separate ossification centres could be detected medial to the optic foramina, but the two orbitosphenoid ossifications simply spread medialwards and invade the posterior extremity of the pars trabecularis, thus constituting the fourth element of the basicranial axis. Similar conditions were encountered in Setifer. It is possible, however, that separate ossification centres in Setifer may have escaped notice, due to the lack of sufficient embryological stages, and that in the latest stage investigated these were already fused with the orbitosphenoids. Were this the case, however, it would afford no additional difficulty, but would merely liken the condition in Setifer to that of Elephantulus, subsequently to be described.

Two "presphenoidal" ossification centres could be distinguished in Elephantulus, one in the medial margin of each optic foramen and quite distinct from, but near the "main" ossification centre of the orbitosphenoid, which was found to be situated in the antero-lateral margin of the optic foramen. These two "presphenoidal" centres, however, were found to coalesce with the "main" orbitosphenoid centres long before they establish continuity with each other in the median plane; moreover, they arise in cartilage which lies at about the junction of the ala orbitalis with the central stem, so that it is not at all certain that they arise in cartilage belonging primarily to the pars trabecularis. On the contrary, it seems much more likely that the strip of cartilage in which they do arise belongs primarily to the ala orbitalis, so that these separate "presphenoidal" centres, if present, merely represent accessory orbitosphenoid

centres which make their appearance in order to hasten the medially extending ossification of the orbitosphenoid.

An exactly similar condition is found in the Rodent, Pedetes (BROOM 1926) and has also been known for long to exist in Man.

The condition found in other Rodents is also of interest, particularly so because the Rodents, as a group, exhibit the best developed "classical" presphenoid. As BROOM (1926) point out, however, there is little doubt that the "presphenoid" in forms like Xerus and Georychus arises from paired lateral centres, as is the case in Pedetes; the only difference being, that in these forms the two centres fuse with each other in the midline before they come to coalesce with the "main" orbitosphenoid ossification centres.

The chief reasons for regarding this fourth element, which appears in the basicranial axis of some Mammals, as completely secondary and having actually nothing to do with the central stem, are: 1. Ontogenetically the central stem of the chondrocranium consists of three definite and constant regions only (the planum basale, the lamina hypophyseos and the pars trabecularis—pars interorbitonasalis). In the ossification of the central stem one would therefore expect three primary ossification centres, and only when placed before irrefutable evidence would one resolve to the contrary. 2. The fact that the basioccipital, basisphenoid and "anterior element" always arise from unpaired median centres, immediately makes one doubt the primary character of the "classical" presphenoid. Indeed, were any one of these basicranial elements to arise from paired centres, one would expect it to be, in the first instance, the basisphenoid, situated in the hypophyseal region, and not an element which arises in the pars trabecularis. 3. The condition prevalent in most members of BROOM's Neotherida, where this problematic element arises from the orbitosphenoid, and, if not directly so, then from paired centres which very soon establish continuity with this bone, makes one strongly suspect its secondary nature, even in forms like Xerus and Georychus, where its true character is somewhat obscured.

Viewed in this light the otherwise complicated composition of the Mammalian basicranial axis becomes quite simple. In all Mammals, as in the Therapsida, it is composed essentially of three elements. viz: 1. The basioccipital, arising from an unpaired centre in the planum basale. 2. the basisphenoid, arising from an unpaired centre in the lamina hypophyseos and 3. The presphenoid (or mesethmoid) which likewise arises from an unpaired centre in the pars trabecularis. This primitive condition, according to our present knowledge, is retained in unobscured form only in the Chrysochloridae. In the remaining Mammals, however, it is obscured by the secondary invasion of the central stem by the orbitosphenoids, which elements have developmentally nothing to do with the central stem. Even the frontals may extend ventrally into the region of the basicranial axis in the case of some Primates (BROOM

1926). But this condition is likewise of pronounced secondary nature (see fig. 68).

Two further considerations arise from the views put forward above: Firstly, the name which the true anterior element of the basicranial axis should bear. It is clear that in Mammals this element has been called both "mesethmoid" and "presphenoid". The latter name, however, was originally used, and also most frequently, in connection with the orbitosphenoid element invading the basicranial axis and it should therefore be retained for this element, provided its significance is fully understood.

The anterior element of the Mammalian basicranial axis undoubtedly represents the homologue of the similar element found in Therapsid Reptiles. As BROOM (1926) points out, a similar element in the Amphibian skull has been given the non-commital name "sphenethmoid" and its possible homologue in birds is called the "ethmoid". As the term "ethmoid" in Mammalian morphology is usually applied to the fused "anterior element" (under discussion) and the two laterally placed pleurethmoids it is advisable to apply another term; this could either be "sphenethmoid" or "mesethmoid". Seeing that the homology of this element goes as far back as the Amphibians where the term "sphenethmoid" is used, this seems to be the obvious name to apply to the Mammalian element.

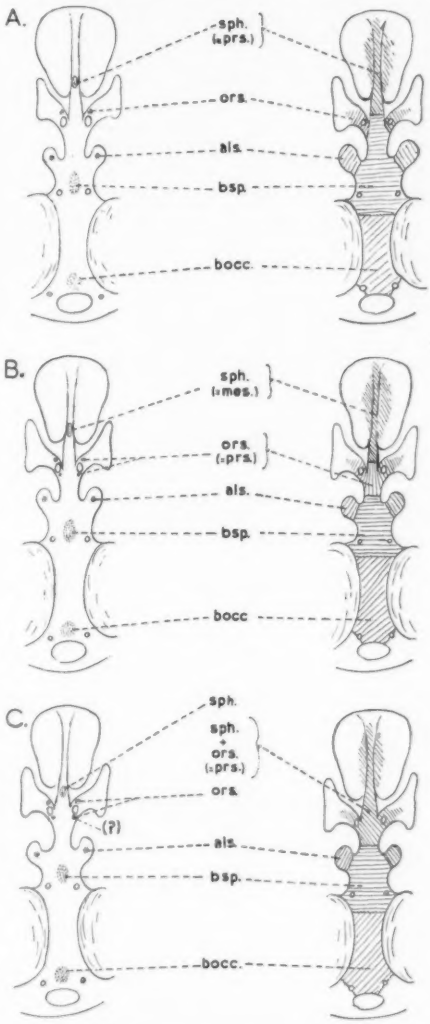

Fig. 68. Diagramatic representation of the composition of the Mammalian basicranial axis, A. Chrysochloridae. B. Broom's Neotheridae. C. Marsupials (and probably also in most other members of Broom's Palaeotheridae). *als.* alisphenoid; *bocc.* basioccipital; *bsp.* basisphenoid; *prs.* presphenoid; *sph.* sphenethmoid (= element known as mesethmoid in some Mammals and presphenoid in others).

In the second instance we feel that, seen in the light of the above discussion, too much taxonomic value has been attached to the composition of the basicranial axis by BROOM. Seeing that the complication of the Mammalian basi-

cranial axis depends, not on an element belonging primarily to the central stem, but on secondary invasion from without, we should guard against a too liberal application of its composition for taxonomic purposes.

5. The anterior paraseptal cartilage: is commonly regarded as a primitive element of the solum nasi, which, in Mammals, became secondarily associated with Jacobson's organ (SPURGAT 1896, SYDEL 1895, GAUPP 1900 and 1908).

The primitive condition in Mammals seems to be a continuous vertically placed lamella (cartilago paraseptalis communis) extending from the lamina transversalis anterior in front, to the lamina transversalis posterior behind. (See STADTMÜLLER 1936, p. 902.) Its connections to the transverse laminae of the solum nasi, however, are held to be secondary. This view is also supported by the fact that in all the animals investigated by the author (Suncus, Elephantulus, Eremitalpa and Setifer) separate blastem and chondrification centres could be distinguished for the anterior paraseptal cartilages. Furthermore, Elephantulus displayed a blastem primordium for the anterior paraseptal which, in the earliest stages, was inseparable from the nasal septum, thus reminding one of the condition prevalent in Didelphys (LEVI 1909) and Canis (OLMSTAED 1911).

That the relations between the anterior paraseptal cartilage and Jacobson's organ are of secondary nature is suggested by the fact that these two structures are very often not co-extensive, a condition well demonstrated in the Golden Mole and also in Suncus, and which in the past has aroused comment from several authors (STURM 1937, CORDS 1915, STADTMÜLLER 1936). Moreover, the ventral and lateral protection of Jacobson's organ formed by the recurved ventral edge of the vertical lamella of the cartilage is acquired secondarily, and is pronounced in the more specialised Mammals only, where it may assume the shape of a deep gutter, affording excellent protection for the organ.

BROOM, since 1898, has regarded the anterior paraseptal cartilage as of considerable importance in determining the affinities of the aberrant Mammals, because, as he maintains, it is but little influenced by the habits of the animals. BROOM laid particular stress on the absence or presence of the "outer bar" which bounds the duct of Jacobson's organ laterally just before it opens into the nasopalatine canal (BROOM 1898, 1902, 1909, 1915, 1938 etc.). The real significance of this "outer bar" has not been determined as yet (see STURM 1937, pp. 207—208), but that it is devoid of any taxonomic value is strongly suggested by its wide and seemingly sporadic occurence amongst Mammals of various orders.

An important embryological point to bear in mind concerning the "outer bar", is that it tends to arise at varying stages of development in different Mammals, and similarly, it may become resorbed again at varying developmental stages, so that one has to be very careful before making any definite

VOL
28
194

statement as to its absence in any particular Mammal (see account given for Suncus, Author, and also account by STURM 1937).

6. The ethmoid: in Mammals is commonly described as arising from three main ossification centres: the medially placed mesethmoid centre which gives rise to the lamina perpendicularis and greater part of the laminae cribrosae of the adult ethmoid, and two laterally placed pleurethmoid centres which give rise to the bulk of the adult ethmoid, the ethmoidal air cells and the turbinals.

It has been held in the past that the medially placed mesethmoid centre represents a neomorph characteristic of Mammals only. BROOM (1926 and 1927), however, has drawn attention to the fact that it is not always present in Mammals, its place being taken in more primitive Mammals by the presphenoid ossification, which is already present in reptiles.

As pointed out before, the development of this region of the skull in Elephantulus, Suncus, Setifer and Eremitalpa led to the conclusion that a neomorphic mesethmoid centre never arises in Mammals but that it always ossifies from the centre already present in Reptiles, which should therefore be called the sphenethmoid. This centre appears relatively late in ontogeny.

The lateral pleurethmoid region of the ethmoid was found to ossify, in all the animals investigated, from several autogenous centres. There is, however, always one main ossification centre in this region which appears relatively early and which is relatively constant in position, always occupying the anterior part of the first primary ethmoturbinal. In addition to this main pleurethmoidal centre several accessory ossification centres were observed, some of which, in the animals investigated, proved to be relatively constant and may be mentioned here.

The most constant and most important of these is the separate ossification centre displayed by the maxilloturbinal of the nasal capsule. The turbinal commonly loses its primary connection with the rest of the pleurethmoid, due to secondary resorption of cartilage, and acquires a secondary attachment to the deep surface of the maxilla. Another fairly constant focus of ossification seems to be the posterior paraseptal cartilage and lamina transversalis posterior. This ossification does not arise from an autogenous centre but emanates from the lateral lamella of the vomer and, on establishing continuity with the rest of the pleurethmoid, it leads to the incorporating of the vomer in the ventral aspect of the ethmoid.

Constant ossification centres were also observed in the nasoturbinal and the processus uncinatus of the crista semicircularis; these centres however, do not retain their separate identity for any length of time before becoming fused with the main pleurethmoid centre. Furthermore, less constant ossification centres seem to be of common occurrence in the second and third primary ethmoturbinals but these do not remain separate from the main centre for long.

The Mammalian ethmoid is commonly regarded as being homologous with the sphenethmoid of Amphibians and with the sphenoid of Crossopterygia (SOLLAS 1914, WATSON 1914, BUTSCHLI 1921 and BROOM 1926). Of the Mammalian turbinals only the maxilloturbinal and nasoturbinal can be traced back to the Reptiles and Birds; the ethmoturbinals, primary and secondary, being neomorphs found only in the Mammalia.

7. The jugal: The relations and significance of this membrane bone in the Mammalian zygomatic arch have been discussed in fair detail particularly by SLADE (1895) and HOGBEN (1919). Nevertheless a few points of morphological interest concerning the jugal have arisen since then and also from the present investigation into the development of the membrane bones in the skulls of Eremitalpa, Setifer, Suncus and Elephantulus, which are worth mentioning here.

The primitive condition of the Mammalian zygomatic arch seems to be somewhat obscure. WEBER (1904) regarded a small jugal in the zygomatic arch as representing the primitive Mammalian condition and, as HOGBEN (1919) remarks: "there can be little doubt that this represents the ancestral condition retained by the class till a date later than that at which the modern lines of Mammalian descent had become differentiated" (p. 77).

The jugal typically joins the zygomatic process of the maxilla in front and the zygomatic process of the squamosal behind, thus completing the zygomatic arch. Apart from these relations, however, it may also establish relations with the lacrimal, alisphenoid and frontal (see WEBER 1927 and 1928 and STADTMÜLLER 1936).

The jugal is peculiar in that it shows a tendency in some Mammalian orders to grow progressively and in others to retrogress. HOGBEN (1919) commenting on the progressive reduction of the jugal in Mammals speaks of the "general tendency among the Mammals for the displacement of the jugal without apparent reference to function at all" (p. 73).

That the state of development of the zygomatic arch is closely associated with the "energy and character of the masticatory process" (SLADE) is no doubt true, but why the jugal should become pushed out of the composition of a zygomatic arch which has not lost its function at all, as is well exemplified by Monotremes and Chrysochloridae, remains completely unexplained. In the Monotremes, Ornithorhynchus presents the more primitive condition. The jugal, being completely absent in Echidna, is represented in the juvenile Ornithorhynchus by a minute element in the anterior upper part of the zygomatic arch where it subsequently becomes completely fused with the maxilla. It does not, however, contribute in any marked degree to the formation of the zygomatic arch which is complete, but formed by the extensive maxillary and squamosal zygomatic processes only.

In Marsupials the zygomatic arch presents a marked contrast to the con-

VOL
28
194

dition prevalent in Monotremes. It is always complete and strongly built and a very well-developed jugal forms its main constituent.

In Chrysochloridae the slender but complete zygomatic arch bears a superficial resemblance to that of the Monotremes, the jugal apparently being completely absent. It differs, however, in that the squamosal does not in the least participate in the formation of the arch. Tracing the development of the Chrysochlorid zygomatic arch, it was found that the so-called zygomatic process of the maxilla ossifies from an autogenous centre, which fuses with the rest of the maxilla at an early stage.

This strongly suggests that the entire arch, which is formed from this centre, is not part of the maxilla at all but actually represents a well-developed jugal. If this is the case, then the resemblance to the Monotreme condition, though superficially close, would actually be very remote. On this interpretation the Chrysochloridae would appear to be specialised, but in a manner very divergent from the Monotremes.

In both the Tupaiidae and the Macroscelidae the zygomatic arch shows a composition not much different from that of the Marsupials—the jugal being constantly present and rather well-defined. Amongst the typical Insectivores the Erinaceidae and Talpidae are held to present a condition of the zygomatic arch not unlike the primitive Mammalian condition: the arch being complete but the jugal small.

A degenerative tendency in the jugal is already noticed in some members of the Erinaceidae (*Erinaceus europaeus* FAWCETT and *Erinaceus microptus* ANDERSON and LECHE). The Centetidae, Solenodontidae and Soricidae present a further advance along this line of specialisation, the zygomatic arch being incomplete or even entirely absent due primarily to the reduction of the jugal. In the Centetidae a rudimentary jugal was found to be represented by the short zygomatic process of the maxilla (LEIMGRUBER 1939 and Author). In the Soricidae and Solenodontidae even a rudimentary jugal seems to be lacking.

Amongst the remaining orders of Mammals the jugal shows definite degenerative changes in the Xenarthra (see WEBER 1928, p. 195), and also in the Manidae, in the latter group of which its reduction may be accounted for by the poorly developed muscles of mastication.

III. TAXONOMIC CONSIDERATIONS.

1. Suncus orangiae and Setifer setosus: The systematic position of Suncus and Setifer as belonging to the typical Insectivores has never been questioned. That they represent related forms, or at least members of the same Order, is clearly demonstrated by the development of their

chondrocrania and by the comparison of these with other members of this Order which have already been investigated.

Thus far the cranial development of the following Insectivores have been investigated: 1. *Talpa europea* (Talpidae), has been thoroughly investigated first by W. K. PARKER (1885) and subsequently by FISCHER (1901), NOORDENBOS (1905) and FAWCETT (1918). BROOM (1915) described the anterior paraseptal cartilages and DAWES (1930) studied the segmentation of the Mole's head. 2. *Sorex vulgaris* (Soricidae), has been studied by W. K. PARKER (1885), LEVI (1909 a and b), DE BEER (1929) and ÄRNBÄCK CHRISTIE-LINDE (1907). 3. *Suncus orangiae* (Soricidae) has been investigated by the author. 4. *Erinaceus europaeus* (Erinaceidae), has been thoroughly investigated by W. K. PARKER (1885), FAWCETT (1918) and MICHELSON (1922). 5. *Tenrec ecuadatus* (Centetidae), has been studied by LEIMGRUBER (1939) and PARKER (1885). 6. *Setifer setosus* (Centetidae), has been investigated by the author. PARKER (1885) described the adult skull.

From the information gained by the above-mentioned investigations it is clear that the cranial development of the typical Insectivores has several points in common which separate them into a distinct and homogeneous group.

The main points of importance are: — 1. The chondrocranium in all the typical Insectivores is relatively straight as compared to the bent type of other Mammals. This is mainly due to the fact that the lamina hypophyseos in early ontogeny does not fuse with the ventral aspect of the anterior extremity of the planum basale but with its anterior tip.

2. The dorsum sellae is always ill-defined and the fossa hypophyseos shallow. This feature can be traced back to the mode of fusion of the lamina hypophyseos with the planum basale.

3. The basicochlear fissure shows a tendency to become reduced and obliterated. In both Sorex and Erinaceus it is completely obliterated although present in the procartilaginous stage of the chondrocranium. In Suncus and Talpa the fissure is subdivided into anterior and posterior divisions by the anterior chordo-cochlear commissure; the posterior division of the fissure becoming obliterated very soon in Talpa. In the Centetidae the fissure is very narrow but still complete.

4. The inferior occipito-capsular fissure also shows a tendency to become reduced in size. In the primitive Erinaceidae it is still well-developed, but in the Talpidae it is much suppressed, and completely obliterated in the Soricidae. In the Centetidae the fissure has lost its separate identity by fusing above with the superior occipito-capsular fissure.

5. A primary suprafacial commissure and foramen are always present. Similarly, a foramen faciale secundarium and secondary suprafacial commissure seems to be almost constantly present, having been described in the Talpidae,

VOL
28
194

Soricidae and Centetidae. In the primitive Erinaceidae, however, it is still deficient.

6. The alicochlear commissure is constantly present and well-developed.

7. The ala temporalis, except in Talpa where it arises in continuity with the central stem, displays an autogenous chondrification centre. The pterygoid process of the ala temporalis is also constantly present, except in Talpa.

8. The ala orbitalis is remarkable in several respects: Firstly the ala hypochiasmata, if not entirely absent, is always small; secondly the pre- and post optic roots of the ala orbitalis, being complete, are always slender; and thirdly the optic foramina are small and slanting and relatively far laterally placed due to the presence of a short common stem which attaches the two optic roots of the ala to the pars trabecularis of the central stem. (In Erinaceidae this stem is ill-defined and in *Sorex vulgaris* it was reported absent due to a secondary fusion of the apex of the ala orbitalis to the cupula posterior of the nasal capsule.)

9. The anterior paraseptal cartilage is always of a rather specialised type with a slender anterior attachment to the lamina transversalis anterior, a strongly laterally recurved vertical lamella which affords ample protection for Jacobson's organ and an "outer bar" which seems constantly present. Its time of appearance, however, and its subsequent resorption is subject to considerable variation amongst members of this group.

10. A cartilago ductus nasopalatini, developing from the anterior paraseptal cartilage and completely fused with it for the support of the nasopalatine duct, is nearly always present. In the Erinaceidae it is, however, rather ill-defined and in the Centetidae entirely absent.

11. A processus opercularis, surmounting the anterior part of the pars canalicularis, is present and well-defined in the more specialised Insectivores—Soricidae and Talpidae—but is absent in the primitive Erinaceidae and also in the Centetidae.

12. The zygomatic arch, if complete, displays a small and ill-defined jugal. The arch is complete only in the primitive Erinacidae and in Talpidae, being deficient in the Centetidae and completely absent in the Soricidae. The jugal shows a simultaneous and parallel reduction, being rudimentary in the Centetidae and almost constantly absent in the Soricidae.

13. The adult basicranial axis is of the more specialised Mammalian type, being composed of the three primary elements found in Therapsid Reptiles, viz basioccipital, basisphenoid and sphenethmoid (mesethmoid). In addition the orbitosphenoids invade the central stem between the basisphenoid and sphenethmoid (mesethmoid) as the presphenoid.

14. The fenestra hypophyseos tends to remain patent until relatively late in ontogeny. This is most marked in the Erinacidae but less so in Talpidae and Soricidae. In the Centetidae, however, the fenestra hypophyseos is oblit-

erated at a very early stage of development as is also the case in the Macroscelidae and Chrysochloridae.

While the Erinacidae, Talpidae and Soricidae seem to represent successive stages in the specialisation of the chondrocranium, the Centetidae and Solenodontidae (which need further investigation) seem to represent a divergent line inside the Insectivores. They retain several primitive features, the most important being: I. The retention of a complete basicochlear fissure. 2. The entire absence of a cartilago ductus nasopalatini. 3. The primitive condition of the fissura metotica, processus recessus and associated structures. 4. The absence of a processus opercularis.

Furthermore the very early obliteration of the fenestra hypophyseos and the development of a pair of well-defined basisphenoidal tympanic wings seem to indicate that the Centetidae, although typical Insectivores, have diverged from the common line of specialisation at a relativly early stage in the phylogenetic history of the group (see fig. 69).

2. Eremitalpa granti: In studying the development of the skull of the Golden Mole one cannot help to note the marked deviation in many important respects from the development and characteristic features of that of the typical Insectivores. Most important amongst these are the following.

1. Unlike Insectivores, the central stem is markedly flexed in the region of the dorsum sellae thus rendering the dorsum sellae more conspicuous and the fossa hypophyseos well-defined. This feature is not characteristic of the Golden Mole but it obtains in most other Mammalian Orders.

2. The alicochlear commissure dose not develop, being not even preformed in procartilage or blastem. This feature seems to represent a specialisation parallel to that encountered in most Primates.

3. The recessus scalae tympani, foramen perilymphaticum and fissura metotica display primitive Monotreme and Reptilian features. The processus recessus is absent in younger stages of development, and in older stages, although present, it is ill-defined so that the recessus scalae tympani remains extracapsular, the fissura metotica undivided, the apertura medialis of the recessus scalae tympani and the fenestra rotunda undefined, and the foramen perilymphaticum opens directly to the exterior of the auditory, capsule.

4. The parieto-occipital commissure is deficient, but in this region the supraoccipital cartilage bears an extensive anteriorly directed wing, which, in later development, ossifies from an autogenous centre, resulting in the formation of an extra bony element (tabular?) in the adult skull.

5. A foramen faciale secundarium is not isolated by the development of a secondary suprafacial (lateral prefacial) commissure.

6. The ala temporalis and also the alisphenoid which arises from it are rather slender and steeply inclined dorsally, so that when completely ossified it still resembles the primitive columella cranii closely.

VOL
28
194

7. The ala orbitalis shows rather primitive relations in that the ala hypochiasmata is extensive but never acquires direct communication with the rest of the ala orbitalis because the pre- and post optic roots remain entirely deficient. The orbitosphenoid ossification emanates from the ala hypochiasmata only.

8. The anterior paraseptal cartilage is primitive in that it remains attached to the lamina transversalis anterior by a broad vertically placed lamella; furthermore it is only slightly recurved laterally for the protection of Jacobson's organ, so that the cartilage as a whole is little more than a vertically placed cartilage lamella. An "outer bar" may appear during later development.

9. A small cartilago ductus nasopalatini is present in the older embryonic stages, but it remains separate from the anterior paraseptal cartilage.

10. The adult basicranial axis is very primitive in that it is composed of three elements only as in Therapsid Reptiles; these elements being the basioccipital, basisphenoid and sphenethmoid (mesethmoid). The orbitosphenoids do not enter into the formation of the adult basicranial axis as is commonly the case in other Mammals.

11. The zygomatic arch is rather specialised being composed entirely by the jugal. The maxilla and squamosal take no part whatsoever in its formation. (Further developmental evidence from other members of the Chrysochloridae is needed to settle this point finally.)

12. A rudimentary surangular is believed to be present near the posterior end of Meckel's cartilage and closely associated with the prearticular (Broom, Cooper etc.). This point also needs further investigation before arriving at any definite conclusions.

13. The head of the malleus is enormously enlarged in many, but not all members of the Chrysochloridae, much more so than in any other Mammal.

14. The basicochlear fissure is present and well-defined.

From the above evidence it is clear that the Chrysochlorids, as far as their cranial morphology is concerned, form a definite unity sufficiently different from the typical Insectivores and any other Order of Mammalia to fully justify their inclusion in an entirely separate Order.

This alteration in the systematic position of the Golden Moles as "Insectivores" has already been strongly advised by Broom (1915 and 1916) and as long ago as 1883 Dobson suggested their "early phylogenetic separation" from other Insectivores, amongst which Centetes was held to be their nearest ally.

That this Mammalion Order is very primitive in several respects is beyond dispute. Indicative of its primitiveness are: 1. The composition of its basicranial axis. 2. Its rudimentary processus recessus and associated structures. 3. The absence of a secondary facial foramen. 4. The primitive nature of both the ala orbitalis and ala temporalis. 5. The unmodified anterior paraseptal

cartilage. 6. The presence of both a surangular and a tabular (of questionable nature).

In spite of these primitive characters the specialised habits of the Golden Moles have lead to their rapid specialisation along lines divergent from any other Mammals. In their cranial morphology this tendency is well reflected by the shape of the skull as a whole—short and broad with enlarged brain case and with short but stout nasal region. Furthermore the composition of the zygomatic arch, the large head of the malleus and the absence of the tensor tympani muscle, the absence of alicochlear commissures, the presence of an extra ossification centre in the supraoccipital cartilage (tabular) and the reduction of the delicate nasal cartilages all point in the same direction.

Taking the Golden Moles as a whole we find that they form a specialised group, which, because of their divergent modifications, are difficult to ally to any other Mammalian Order. That they have, however, become isolated from remaining Mammals, presumably from the ancestral Insectivore stock, at a very early period is unquestionable as they still retain several of the most primitive Mammalian features in their skulls.

3. Elephantulus myurus jamesoni: Taking Elephantulus as an example of the Macroscelidae we find that the chondrocranium is typically like that of Placental Mammals and bears no close resemblance to the characteristic Marsupial chondrocranium. The Marsupial affinities recognised by Parker (1885), Elliot, Smith (1902), Gregory (1910) and Broom (1902, 1915 a and b) are to be regarded as perhaps of secondary, and definitely of subordinate importance.

The most characteristic features of the Macroscelid chondrocranium can be briefly summarized as follows:

1. The central stem of the chondrocranium, during the earlier developmental stages, shows a marked flexure in the region of the dorsum sellae. In this respect thus, it contrasts sharply with the typical Insectivores and resembles the Chrysochloridae. This flexure, however, rapidly straightens out during later development so that, as in typical Insectivores, the dorsum sellae is inconspicuous and the fossa hypophyseos shallow.

2. The fenestra hypophyseos becomes obliterated very early in ontogenetic development, unlike the typical Insectivores, yet resembling the Chrysochloridae.

3. The secondary suprafacial commissure (lateral prefacial commissure) is deficient as in the Chrysochloridae.

4. The inferior occipito-capsulare fissure is present but very narrow.

5. The basicochlear fissure is present and not subdivided.

6. The alicochlear commissure is present and well-defined.

7. A processus tympanicus petrosi caudalis as well as a rostral entotympanic

VOL 28 194

and possibly a caudal entotympanic are present and partake in the formation of the osseous bulla.

8. The ala temporalis displays a foramen alisphenoidale only. Furthermore it bears a very conspicuous pterygoid process which arises ontogenetically from a separate centre.

9. A processus tympanicus allisphenoidei appears in later development.

10. The ala orbitalis displays thick and well-defined pre-and post optic roots which attach, independantly of each other, to the pars trabecularis of the central stem; they bound a very large optic foramen. The ala hypochiasmata, which is absent in later development, is present in blastem only.

11. The anterior paraseptal cartilage is of a relatively primitive composition, being attached in front to the lamina transversalis anterior by a wide base. Furthermore, the vertical lamella is only slightly recurved laterally. An "outer bar" is present and well-defined. A cartilago ductus nasopalatini is entirely absent.

12. The zygomatic arch is complete and strong and a well-developed jugal participates in its formation.

13. As in the typical Insectivores, the adult basicranial axis is composed of four elements, viz: the basioccipital, basisphenoid, presphenoid (derived from orbitosphenoids) and the sphenethmoid (mesethmoid).

14. An opercular process is absent.

In comparing the chondrocrania of the Tupaiidae (HENCKEL 1928) with that of the Macroscelidae one is bound to admit that the similarity is indeed so striking that any effort to split up the Menotyphla and separate the Tupaiidae, from the Macroscelidae is artificial. It will be recalled that LE GROS CLARK (1932), who, like SIMPSON (1931) abandons the distinction of Lipotyphla and Menotyphla, separates the Tree-shrews and Elephant-shrews placing them in separate super-families. This is done because: "it would be difficult to conceive two small Mammalian brains which are more fundamentally different and divergent in their structure than those of Macrosceledes and Tupaia".

CARLSSON (1909 and 1922) likewise expressed the opinion that the Tupaiidae and Macroscelidae are no near allies and she therefore provisionally links the Macroscelidae to the Erinaceidae, regarding the Tupaiidae (1922) as a sub-order of the Prosimiae. This view, however, cannot be supported on data derived from the development of the skulls in these forms.

The chondrocrania of the Tupaiidae and Macroscelidae differ only in a few minor respects of seemingly little significance. They are the following:

1. The anterior paraseptal cartilage in the Tupaiidae is slightly more specialised than in the Macroscelidae. An "outer bar" is absent in Tupaiids according to HENCKEL (1928) but this does not signify that it will not appear in later development, furthermore the "outer bar" seems to be devoid of any taxonomic significance (vide Supra).

2. The ala temporalis in Tupaiidae does not display a separate foramen alisphenoidale, neither is a processus pterygoideus developed. This latter process, however, being exceptionally well-developed in Macroscelids, arises in this latter group from an autogenous centre and fuses with the rest of the ala temporalis relatively late. Moreover, it is closely associated with the pterygoid cartilage, and it is therefore possible that in the relatively young specimen of *Tupaia javanica* investigated by HENCKEL this process was not yet fused with the ala temporalis but closely associated with the pterygoid cartilage.

3. The occipito-capsular fissures are more compressed in the Tupaiids than is the case in the Macroscelidae.

4. The orbito-parietal commissure which, in the Tupaiidae is still complete, is deficient in the Macroscelidae—a difference of very little, if of any, phylogenetic significance.

5. The composition of the auditory bulla in the Tree- and Elephant-shrews is slightly different. In the former it is formed for the greater part by the entotympanic, being supplemented only in minor degree by the alisphenoid and perhaps the basisphenoid (VAN DER KLAAUW 1929), whereas in the Macroscelidae the bulla is formed by the two entotympanics (caudal and rostral) supplemented by the alisphenoid, basisphenoid, petrosum and tympanicum (ectotympanic).

Morphological evidence accumulating in the last 30—40 years (GREGORY 1910, 1930; KAUDERN 1910; VAN KAMPEN 1904; CARLSSON 1922: LE GROS CLARK 1924 a—b, 1925, 1926, 1932, 1934; SIMPSON 1931 a—b; SCHWALBE 1923; OSSENKOPP 1925; SMITH 1927) have all pointed towards a closer alliation between the Tupaiidae and primitive Primates than was previously believed to be the case. So conclusive was the evidence in some respects that CARLSSON (1922), WOOD JONES (1929) and LE GROS CLARK (1934) thought it reasonable to finally remove the Tupaiidae from their associations with the Insectivores and to include them among the Primates of which they were believed to represent extremely primitive forms.

Opinions to the contrary, however, have also been expressed by LORENZ (1927), HENCKEL (1928 a—b), VAN DER KLAAUW (1929). These authors find sufficient evidence, particularly from the cranial development (HENCKEL and VAN DER KLAAUW) to support the classical alliation of the Tupaiids with the Insectivores.

From our own investigation into the development of the Macroscelid skull, which resembles that of the Tupaiidae very closely (vide Supra), we are convinced that it was impossible for a Primate skull to have developed from this type, which, in many important respects, proves to be already on the Insectivore line of specialisation. HENCKEL (1928, p. 226) expresses the following opinion: "Nach allen unseren morphologischen Vorstellungen muss es als völlig ausgeschlossen gelten, dass, wenn die Schädelentwicklung einmal so

VOL
28
194

weit in eine bestimmte Richtung—Tupaja—gelenkt ist, sie noch in der Lage ist ein Endergebris zu liefern, das—Primatenschädel—eine völlige andere Genese voraussetzt".

It is unnecessary to discuss the morphological evidence dealt with by HENCKEL anew, but our own investigation into the Macroscelid skull, as well as that of VAN DER KLAAUW (1929) supports this view very strongly.

The seemingly close affinities which the adult skulls of the Tupaiids and Lemuroids display (GREGORY 1910) are due, as it seems, for the greater part to parallel modifications on account of their arboreal habits.

Regarding the affinities of the old Menotyphla with the typical Insectivores our investigations have led to the following conclusions:

The relatively straight stem of the chondrocranium with the associated depression of the dorsum sellae and fossa hypophyseos in the Tupaiids and Macroscelidae as in the Insectivores, seems to signify that this is a relatively old feature of the Insectivore chondrocranium which it shares with the Menotyphla but which arose after these have become distinct from the Primates and also from the Chrysochloridae. Also the general shape and outline of the chondrocranium of the Menotyphla is not at all unlike that of Insectivores, but it contrasts sharply with that of the Primates where the nasal region is much reduced and the cranial cavity expanded.

That the Menotyphla became separated from the primitive Insectivore stem very early and then developed along divergent lines, is strongly suggested by the following evidence:

1. The zygomatic arch in the Tupaiidae and Macroscelidae is strongly built and unlike Insectivores, which shows a degenerative tendency of the arch and of the jugal in particular, the jugal in these forms is very well defined and shows progressive development, forming the greater part of the arch and even encroaching on the glenoid cavity in some forms.

2. The tympanic region and the development and composition of the auditory bulla in Tupaiids and Macroscelidae show that they represent a divergent line of development which has become separated from the Insectivore line very far back in their phylogenetic history.

3. The ala orbitalis of the Tupaiids and Macroscelidae is in every respect different from that of all typical Insectivores. The pre- and post optic roots of the ala orbitalis are very well developed, join the pars trabecularis separately, and bound a large and spacious optic foramen; the ala hypochiasmata is missing. As a consequence we find that the optic foramen, which in typical Insectivores has the shape rather of a small slanting canal floored by the ala hypachiasmata and placed relatively far laterally, is in the Tupaiidae and Macroscelidae a large straight-forward foramen without any floor and placed directly next to the central stem.

4. The cochlear capsules in Tupaia and Macroscelides converge more

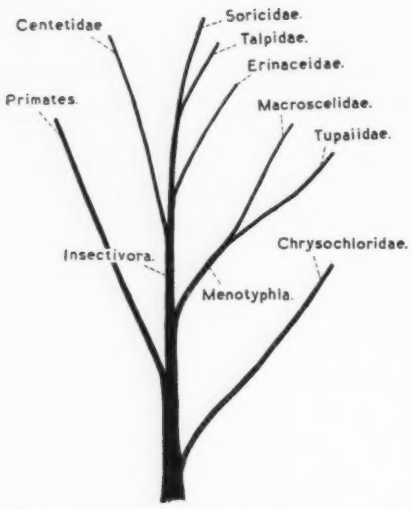

Fig. 69. Diagramatic representation of the possible affinities of the Primates, Insectivores, Menotyphla and Golden Moles

strongly anteriorly than is the case in any of the typical Insectivores. Consequently the anterior part of the planum basale is much narrower and more compressed in these, while the lamina hypophyseos seems to be relatively much wider and the internal carotid foramina farther laterally placed.

This being the main evidence indicating the separate identity of the old Menotyphla, there are other primitive features in the chondrocranium which distinguish them from the general trend of the Insectivore line of specialisation. Most important amongst these are; 1. The absence of a secondary facial foramen and suprafacial bridge. 2. The retention of a well-defined basicochlear fissure. 3. The relatively primitive form of the anterior paraseptal cartilage. 4. The very early obliteration of the fenestra hypophyseos.

The development of the skull, therefore, supplies ample justification for regarding the Menotyphla as a separate Order, distinct from, but allied most closely to the Insectivores.

In conclusion we arrive at the general decision that the polymorphic Insectivore Order, in its classical form, is no longer tenable as such. The Chrysochloridae have to be placed in a separate Order which is believed to have become differentiated from the very primitive Mammalian stock even before the Primates and Insectivores became distinct.

Furthermore, the Menotyphla are separated from the Insectivores and put in a definite Order by themselves. They are however, believed to have become distinct from the primitive Insectivore stock long after the Primates became separated from it. The Insectivore Order, thus, as we hold it now, comprises only the old Lipotyphla of HAECKEL, except that the Chrysochloridae have become excluded.

The view put forward above is summarized in the above standing diagram (see fig. 69).

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VOL
28
194

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VOL
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194

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KEY TO LETTERING.

a.ai. arteria alveolaris inferior.
a.aob. apex of ala orbitalis.
a.asc. ampulla of anterior semicircular canal.
acc. alicochlear commissure.
accc. anterior chordocochlear commissure.
a.ccom. arteria carotis communis.
a.ci. arteria carotis interna.
ah. ala hypochiasmata.
a.io. arteria infra-orbitalis.
al. atlas.
als. alisphenoid.
a.lsc. ampulla of lateral semicircular canal.
alrst. apertura lateralis of recessus scalae tympani.
alt. ala temporalis.
alw.so. antero-laterally directed wing of supra-occipital cartilage.
a.mm. arteria meningia media
am.rst. apertura medialis of the recessus scala tympani.
aob. ala orbitalis.
a.opt. arteria ophthalmica.
a.pal. arteria palatina.
a.p.as. anterior spur of processus alaris superior.
apc. anterior paraseptal cartilage.
ap.dt. articular process of dentary.
app. anteriorly directed spur of parietal plate.
apso. anterior prolongation of supraoccipital (= "processus opercularis" of FAWCETT).
aqc. aquaeductus cochlea (= ductus perilymphaticus).
ar.et I. anterior root of first primary ethmoturbinal.
asc. anterior semicircular canal.
as. et I. anteriorly directed spur of first primary ethmoturbinal.
a.st. arteria stapedialis.
a.stap. arteria stapedialis.
at. atrioturbinal.
b.a.mm. branch of arteria meningea media.
blv. bloodvessel.
b.occ. basioccipital.
bp. basal plate.
br. brain.
br.a.mm. branches of arteria meningea media.
br.a.stap. branch of arteria stepedialis.
bs. basis stapedis.
bsp. basisphenoid.
bvc. basivestibular commissure.
ca.nc. cupula anterior of the nasal capsule.
cba. commissura basicochlearis anterior.
cbi. crus breve incudis.
cbp. cribriform plate.
cc. cochlear capsule.
c.cbp. cut end of cribriform plate.
ccm. crus commune of anterior and posterior semicircular canals.
c.dnl.at. canal for nasolacrimal duct piercing the atrio-turbinal.
cf. crista falciformis.
cg. crista galli.
ci. corpus incudis.
ci.cb. crista intercribrosa.

cli. crus longum incudis.
cm. caput mallei.
cnp. cartilago ductus nasopalatini.
cocp. commissura occipito-capsularis posterior.
cop. commissura orbito-parietalis.
cpc. commissura parieto-capsularis.
cpca. commissura parieto-capsularis anterior.
cpl. cavum perilymphaticum.
cp.nc. cupula posterior of the nasal capsule.
cpo. commissura parieto- occipitalis.
cr. canalis reuniens.
crp. crista parotica.
cr.smc. crista semicircularis.
cs. canalis singulare.
csc. cavum supracochleare (= hiatus spurius).
csbp. cut surface of planum basale.
csph. commissura sphenethmoidalis.
cst. central stem.
csto. common stem for taeniae opticae.
ct. chorda tympani nerve.
cta. cartilago tubae auditivae.
ctn. cut end of tectum nasi.
c.tpn. cut end of tectum posterior nasi.
cus. canalis utriculo-sacularis.
cvc. cavum cochleare.
cvcl. cavum canaliculare.
cv.in. cavum internasale.
cvv. cavum vestibulare.
dc. ductus cohclearis.
dbl. diffuse blastem
de. ductus endolymphaticus.
d.gnl. duct of glandula nasalis lateralis.
dl. et I. dorsal lamella of first primary ethmoturbinal.
dnl. ductus nasolacrimalis.
dnp. ductus nasopalatini.
dnph. ductus nasopharyngeus.
dp. deep petrosal nerve.
ds. dorsum sellae.
d.snt. deficiency at base of sulcus above root of nasoturbinal.
dz.dnl. deficiency in zona annularis for exit of ductus nasolacrimalis.
eam. external auditory meatus.
Et. Eustachian tube.
et I. first primary ethmoturbinal.
et II. second primary ethmoturbinal.
et III. third primary ethmoturbinal.
ex.occ. exoccipital.
f. frontal.
fa. foramen for artery.
fai. foramen acusticum inferius.
fals. foramen alisphenoidale.
fas. foramen acusticum superius.
fba. fenestra basalis.
fbc. fissura basicochlearis.
fbca. fissura basicochlearis anterior.
fbcp. fissura basicochlearis posterior.
fc. foramina cribrosa.
fc.ppc. flange of thin cartilage surmounting the posterior paraseptal cartilage.
fe. foramen endolymphaticum.
fen.hy. fenestra hypophyseos.
f.eph. foramen epiphaniale.
ffs. foramen faciale secundarium.
fhy. fossa hypophyseos.
fi. fossa incudis.
fj. foramen jugulare.
fjs. foramen jugulare spurium.
fls. foramen for lower nerve to saccule.
fm. foramen magnum.
fn. fenestra narium.
fo. foramen ovale (= foramen vestibuli).
foci. fissura occipito-capsularis inferior.
foc. fissura occipito-capsularis.
focs. fissura occipito-capsularis superior.
f.olf. fila olfactoria.
fon. fissura orbitonasalis.
fop. foramen opticum.
fo.rmd.V. foramen ovale for mandibular nerve.
fp. foramen perilymphaticum.
f.pc. foramen prechiasmaticum.
fpr. foramen perilymphaticum.
fpt. foramen pretransversale.
frd. fenestra rotunda.
fsi. foramen singulare.
fsii. fossa subarcuata inferior interna.
fsn. fenestra superior nasi (= foramen dorsale).
fssc. fossa subarcuata superior externa.
fssi. fossa subarcuata superior interna.
fvl. foramen in vertical lamella of anterior paraseptal cartilage.
g.VII. ganglion of facial nerve.
g.VIII. ganglion of auditory nerve.

VOL 28 194

gcnf. ventral groove in cartilago ductus nasopalatini for nasopalatine duct.
gg. Gasserian ganglion.
ggn. ganglion geniculi.
gl. gland.
gnl. glandula nasalis lateralis.
gsp.n. greater superficial petrosal nerve.
h.i. head of incus.
hl.apc. "horizontal lamina" of anterior paraseptal cartilage.
hp. hypophysis.
h.pt. hamulus of pterygoid.
hs. head of stapes.
hy. hyoid (= Reichart's cartilage).
hy.for. hypoglossal foramen.
iam. internal auditory meatus.
ic. incus.
icf. foramen for the internal carotid artery.
id. incipient subdivision of foramen acusticum inferius.
iic. incisura intercondyloidea.
ijv. internal jugular vein.
im.at. incisura maxillo-atrioturbinalis.
i.n.np. incisura for nervus nasopalatinus.
i.o. incisura ovalis.
isr. inferior secondary recess of recessus superior (v. frontalis).
i.tpo. incomplete taenia postoptica.
Jd. Jacobson's duct.
Jo. Jacobson's organ.
lac. lacrimal bone.
lal. lamina alaris.
l.cr. lamina cribrosa.
lhy. lamina hypophyseos.
l.ic. lamina infraconchalis.
ljv. lateral jugular vein.
llv. lateral limb of vomer.
l.mt.mx. line of fusion between maxilloturbinal and maxillary bone.
lns. lower nerve to saccule.
lob. ligamentous "outer bar".
ls. lamina spiralis.
lsc. lateral semicircular canal.
lsp. lesser superficial petrosal nerve.
lta. lamina transversalis anterior.
ltp. lamina transversalis posterior.
m. malleus.
Mc. Meckel's cartilage.
mcs.apc. medially directed cartilaginous shelf of anterior paraseptal cartilage.
md.n. mandibular nerve.
md.p.lv. medially facing deficiency in processus lateralis ventralis.
mit. milk incisor tooth.
mm. manubrium mallei.
mmt. milk molar tooth.
m.rcl. musculus rectus capitis lateralis.
mr. et I. medial root of first primary ethmoturbinal.
msr. medial secondary recess of recessus superior.
m.stap. musculus stapedius.
mt. maxilloturbinal.
m.temp. musculus temporalis.
m.tp. musculus tensor palati.
m.tt. musculus tensor tympani.
mx. maxilla.
mxl.n. maxillary nerve.
n. nasal.
napsc. nerve to ampulla of posterior semicircular canal.
n.aud. nervus auditorius.
nc. notochord.
ncp. nasal capsule.
n.fac. nervus facialis.
n.hy. nervus hypoglossus.
nm. neck of malleus.
n.np. nervus nasopalatinus.
n.o. nervus opticus.
n.pm. nervus palatinus major.
n.pme. nervus palatinus medius.
nsc. nodule of secondary cartilage in palatine process of maxilla.
nt. nasoturbinal.
n.tg. nervus trigeminus.
n.v. nervus vidianus or nerve of the pterygoid canal.
oacp. ossified anterior clinoid process.
oap. et I. ossified anterior process of first primary ethmoturbinal.
ob. "outer bar".
oc. occipital condyle.
oc.apc. ossification centre in anterior paraseptal cartilage.
occ.cd. occipital condyle.
o.chi. optic chiasma.
o.cr.smc. ossified portion of crista semicircularis.
o. et I. ossified first primary ethmoturbinal.

of. optic foramen.
ojd. site of opening of Jacobson's duct.
olf.nf. olfactory nerve fibres (fila olfactoria).
o.mt. ossified maxilloturbinal.
o.nt. ossified nasoturbinal.
o.pn. ossified paries nasi.
o.pr. ossified presphenoidal region of central stem.
opt.n. ophtalmic nerve.
o.pu. ossified processus uncinatus.
orcma. openings leading to resorbtion cavity in massa angularis.
os. orbitosphenoid.
osc.alt. ossification centre in the ala temporalis.
ot.g. otic ganglion.
o.ty. os tympanicum (ectotympanic).
p. palatine.
pa. prearticular (gonial).
p.ai. processus alaris inferior.
p.al. processus alaris.
p.al.alt. processus antero-lateralis of ala temporalis.
par. parietal.
p.as. processus alaris superior.
pb. planum basale.
pbc. posterior basicochlear commissure.
pc. pterygoid cartilage.
pcc. prominentia cruris communis.
pctl. tract of procartilage.
p.cp. processus cupularis.
pcs. procartilage strip.
pff. primary facial foramen.
pf.mx. processus frontalis of maxilla.
pl.os. pleurethmoid ossification.
p.lv. processus lateralis ventralis.
pm. promontorium.
pmx. premaxilla.
pn. paries nasi.
p.o. processus opercularis.
poa. prominentia anterior.
pocc. pila occipitalis.
poi. prominentia inferior (= prominentia maxillaris).
posp. prominentia superior (= prominentia frontalis).
pp. parietal plate.
p.pac. processus paracondyloideus.
pp.alt. pterygoid process of ala temporalis.
ppc. posterior paraseptal cartilage.
pp.cup. posterior spur to cartilago ductus nasopalatini (= cartilago palatini).
p.p.cp. primordium of processus cupularis.
pp.mx. palatine process of maxilla.
p.pt. processus pterygoideus.
p.rec. processus recessus.
pr. et. I. posterior root of first primary ethmoturbinal.
psa. prominentia semicircularis anterio:
psc. posterior semicircular canal.
pscc. prominentia supraconchalis.
p.sfc. primary suprafacial commissure
psl. prominentia semicircularis lateralis.
psp. prominentia semicircularis posterior.
pstf. primary stylomastoid foramen.
pt. pterygoid.
ptr. pars trabecularis of central stem.
p.ty. posterior extremity of tympanic cavity.
p.ty.bsp. processus tympanicus basisphenoidei.
p.ty.pc. processus tympanicus petrosi caudalis.
p.u. processus uncinatus.
pua. prominentia utriculo-ampullaris anterior.
pual. prominentia utriculo-ampullaris lateralis.
puap. prominentia utriculo-ampullaris posterior.
pv.pmx. processus prevomeralis of premaxilla.
pxn.pmx. processus extranasalis of premaxilla.
r.acc. rudimentary alicochlear commissure.
rcma. resorption cavity in massa angularis.
rdpn. resorption deficiency in paries nasi.
rdsn. resorption deficiency in septum nasi.
rdtn. resorption deficiency in tectum nasi.
rec.ant. recessus anterior.
rec.cup. recessus cupularis.
rec.sc. recessus supraconchalis.
ri. recessus inferior (= recessus maxillaris).
rmd.V. ramus mandibularis V.
rmx.V. ramus maxillaris V.
r.p.as. root of processus alaris superior.
rsal. recessus supra-alaris.
rst. recessus scala tympani.
ruaa. recessus utriculo-ampullaris anterior.

rual. recessus utriculo-ampullaris lateralis.
ruap. recessus utriculo-ampullaris posterior.
rve.apc. recurved ventral edge of anterior paraseptal cartilage.
sac. saccule.
sal. sulcus antero-lateralis.
sa.p. et I. sulcus corresponding to attachment of the anterior root of the first primary ethmoturbinal.
sbc. sulcus basicochlearis.
scs.fsn. short cartilaginous spur dorsal to fenestra superior nasi.
set I. first secondary ethmoturbinal.
set II. second secondary ethmoturbinal.
set III. third secondary ethmoturbinal.
sf. foramen in stapes.
sfac. sulcus facialis.
sldn. sulcus dorsalis nasi.
slvn. sulcus ventralis nasi.
smxl.g. submaxillary ganglion.
sn. septum nasi.
snl. sulcus for ductus nasolacrimalis.
snt. sulcus corresponding to attachment of the nasoturbinal.
so. supraoccipital cartilage.
s.occ. supraoccipital ossification.
so. et II. sulcus corresponding to attachment of the second primary ethmoturbinal.
sp. et III. sulcus corresponding to attachment of the third primary ethmoturbinal.
spf. septoparaseptal fissure.
sp.fo. spheno-parietal fontanella.
spl. sulcus postero-lateralis.
spl.g. sphenopalatine ganglion.
sq. squamosal.
sr. et I. superior root of first primary ethmoturbinal.
ss. sulcus for stapedial artery and part of internal carotid artery.
s.sep. sulcus septalis.
ss. et I. sulcus corresponding to attachment of first secondary ethmoturbinal.
ss. et II. sulcus corresponding to attachment of second secondary ethmoturbinal.
s.sfc. secondary suprafacial commissure (= postpalatine commissure).
ssr. superior secondary recess of recessus superior (v. frontalis).
s.stap. sulcus stapedialis (= sulcus musculi stapedii).
ssup. sinus superior.
st. stapes.
t.hy. tympanohyale.
tljv. trough for lateral jugular vein.
t.m.stap. tendon of musculus stapedius.
tn. tectum nasi.
tpn. tectum posterior nasi.
tpo. taenia postoptica of ala orbitalis.
tprco. taenia preoptica of ala orbitalis.
tt. tegmen tympani.
ty. tympanic cavity.
ut. utricle.
v. vomer.
vc.os. ventral crest on orbitosphenoid.
Vd.n. Vidian nerve.
vl.apc. vertical lamella of anterior paraseptal cartilage.
vl. et I. ventral lamella of first primary ethmoturbinal.
za. zona annularis.

VOL
28
194

SOME NEW INTERPRETATIONS OF THE SKULL IN POLYPTERUS

BY

TORSTEN PEHRSON

(With 28 figures in the text.)

VOL.
28
1947

CONTENTS.

Introduction 400

Notes on the Chondrocranium 401

Cartilage Bones 404
Sphenoid 404
Occipital 404
Autosphenotic 404
Ectethmoid 405
Opisthotic 405
Prootic 405
Mento-mandibular 405
Articular 405
Hyomandibular and Accessory Hyomandibular 406

The Sensory Line System 407

The Sensory Canal Pattern in Polypterus, Holosteans and Palaeoniscids 413

Development of Dermal Bones 425
Nasal 426
Frontal 430
Rostral 431
"Premaxillary" and Antorbitals 431
Lacrimal 433
"Maxillary" and Infraorbitals 434
Quadrato-jugal 436
Postorbital 438
Dermosphenotic 438
Intertemporo-supratemporo-parietal 438
Extrascapulars 441
Suprascapulars 442
Supracleithral 443
Dentary-splenial 443
Angular-splenial 444
Coronoids and prearticular 444
Preopercular 445
Vomer 448

Dermopalatine, Ecto- and Entopterygoid 448
Metapterygoid 448
Parasphenoid 449
Summary 449
Bibliography 451
Key to Text-figures 454

INTRODUCTION.

The systematic position and phylogenetic relations of *Polypterus* have been the subject of varying interpretations since HUXLEY (1861) established the group he named *Crossopterygii* for *Polypterus* and *Osteolepis*. POLLARD (1891) has tried to trace the relationships of this fish on one side to the most archaic *Selachii* and on the other to Stegocephalians and Amphibians. GOODRICH has demonstrated in various papers that *Polypterus*, according to his results, is more nearly related to the Actinopterygians than to the Osteolepids (1907, 1908, 1909 and 1919). Later he has emphasised the close resemblance with the Palaeoniscids (1928), an opinion that has been maintained by several later authors. Thus, MOY-THOMAS (1933, a and b) considers *Polypterus* to be a "specialised Palaeoniscid which has survived to the present day". Recently JARVIK (1943 and 1947) has called to life HUXLEY's original opinion of *Polypterus* being a Crossopterygian, only more specifically a Coelacanthid, or at least more closely resembling these fishes.

A great obstacle to an understanding of many features in the adult *Polypterus* has been the lack of suitable embryological stages. BUDGETT's in so many ways epoch-making material comprised, apart from very young stages, only specimens where the skull is already practically formed, and not only the chondrocranium but unfortunately also the dermal skull. The structure of the fins made HUXLEY once establish the group Crossopterygians, but it seems to be the superficial resemblance of the skull of *Polypterus* to the Coelacanthid skull that chiefly causes the present day classification of this fish amongst the Crossopterygians, and a shortage of embryological evidence has left the field open for surmises, impossible to refute in earnest.

Lately the author has had the opportunity of examining a series of comparatively young specimens of *Polypterus senegalus* collected by the swedish Gambia-expedition in 1932 by Dr. GUSTAV SVENSSON. Whereas the smallest specimen of the "old" series in BUDGETT's collection measured 30 mm, the smallest in SVENSSON's measured only 24 mm and is, thus, the youngest *Polypterus senegalus* so far known above BUDGETT's 9.3 mm specimen. It proved to be just the age when many af the dermal bones in the skull were forming.

The investigation has been carried out in the Zootomical Institute of the University of Stockholm. The youngest stages measured 24, 27 and 29 mm

VOL
28
194

respectively, but besides those a number of stages of different length have been available. Further two specimens of *P. bichir* 45 and 125 mm in length as well as one of *P. lapradei* measuring 80 mm have been used. All specimens were excellently fixed in BOUIN's fluid and in very good condition. They have been laid in complete series of transverse sections of 7 to 8 my in thickness.

NOTES ON THE CHONDROCRANIUM.

The chondrocranium of the 24 mm specimen, the youngest at hand, differs only in some insignificant details from the cranium of BUDGETT's 30 mm specimen re-described by MOY-THOMAS (1933). Thus, for instance, the epiphyseal bridge is not yet closed in the 24 mm specimen (fig. 1).

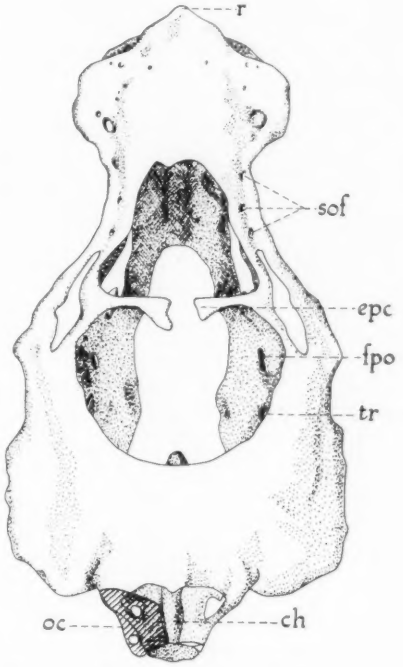

Fig. 1. *Polypterus senegalus,* 24 mm. Chondrocranium in lateral view (24×1). Striped areas, chondral bones. For lettering, see p. 454.

The rostral projection seems to be more sharply modelled in the 24 mm specimen (fig. 2) than is shown by the reconstruction as represented by MOY-THOMAS in the 30 mm. As a matter of fact, it has the same shape in later stages as well (figs. 3 and 4). The author has thus been unable to corroborate LEHN's (1918) statement that the rostrum is divided into a dorsal and a ventral process surrounding the ethmoidal cross commissure of the infraorbital sensory canal. The author has also examined a specimen of the same species and the same length (76 mm) as LEHN (fig. 4) without having been able to discover any division of the rostral process. A slight indentation is found in the adult specimen of *Polypterus bichir* represented by ALLIS (1922), and is probably due to the development of the rostral bone.

LEHN's statement is quoted by DE BEER (1937) and more recently by JARVIK (1942), who discusses the morphological value of the two alleged rostral processes. The question of the rostrum has a certain morphological interest as in, for instance, *Chlamydoselachus* the rostral commissure of the infraorbital canal runs ventrally to the rostrum, but, in Actinopterygians (including *Polypterus*) dorsally. In a 42 mm *Acipenser,* examined by the author, the commissure

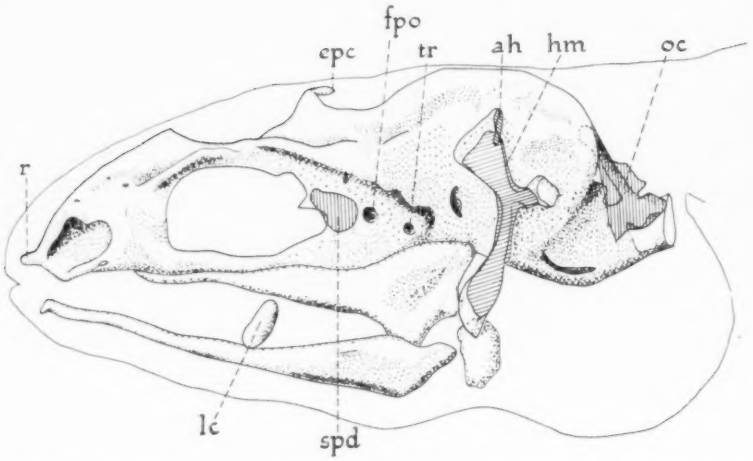

Fig. 2. *Polypterus senegalus*, 24 mm. Chondrocranium in lateral view (24×1). Striped areas, chondral bone. For lettering, see p. 454.

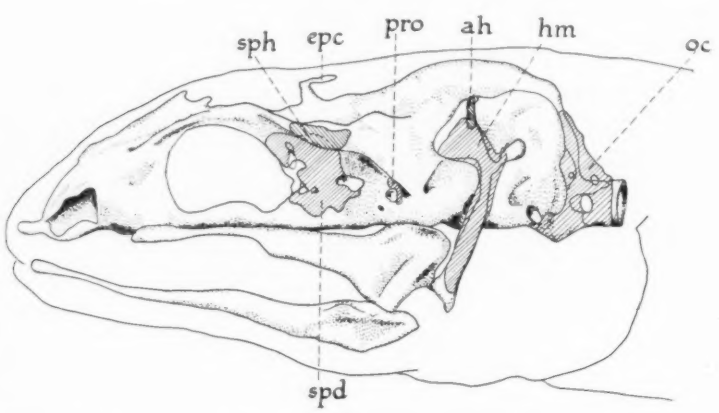

Fig. 3. *Polypterus senegalus*, 37 mm. Chondrocranium, lateral view (16×1).

canal pierces the tip of the rostrum, although in old specimens (ALLIS 1904) it is situated dorsally near the anterior end of the rostrum. In still younger specimens of *Acipenser* it lies anteriorly and slightly dorsally to the tip of the rostrum.

These conditions indicate a certain movableness of the rostral canal. The canal is independent of the chondrocranium, and its position in the anterior end of the snout allows a course dorsally to, ventrally to, or even through the rostrum, the rostral tissue in the last case having grown round the canal. JARVIK has attached a certain importance to the question of the existence of a "dorsal" or a "ventral" rostral process in *Polypterus*. Notwithstanding the

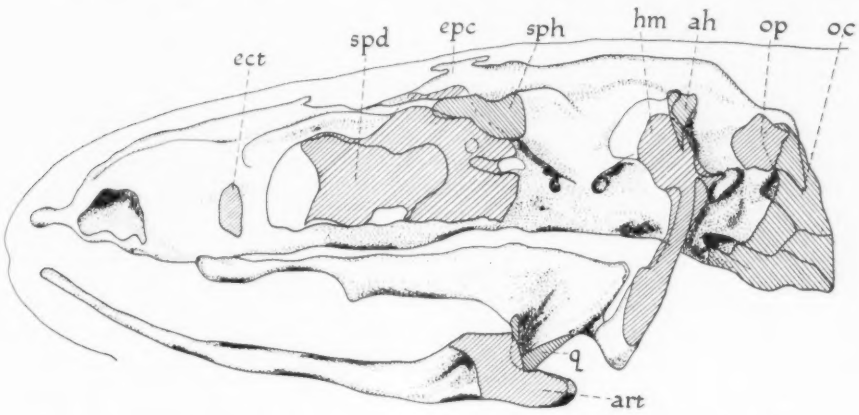

Fig. 4. *Polypterus senegalus*, 76 mm. Chondrocranium, lateral view (11.5×1).

VOL. 28 1947

fact—as shown by the present author—that there is no divided rostrum in this fish the question of a "dorsal" or a "ventral" rostrum is no problem at all, as it is simply reduced to the question of the course of the rostral canal.

In *Euporosteus*, a fish JARVIK refers to for the alleged resemblance between *Polypterus* and the Coelacanthids (l.c., p. 609) the rostral canal crosses the tip of the snout in a groove, but, a rostrum can hardly be said to exist in this fish.

JARVIK also mentions (l.c., p. 260) that the foramen for ramus buccalis is to be regarded as a part of the so-called fenestra endonarina communis "bounded off from this fenestra comparatively late during the embryonic development". The reason should be that the foramen is not shown in the MOY-THOMAS reproduction of the 30 mm specimen whereas it is to be seen in LEHN'S reconstruction of a 76 mm specimen. As a matter of fact this foramen exists in a 30 mm specimen, even in a 24 mm specimen (fig. 1), but is situated so far ventrally that it does not show in a profile reconstruction.

The branchial skeleton in the adult has been dealt with thouroughly by ALLIS (1922), and in addition MOY-THOMAS (1933) has given a brief account followed by schematic diagrams of the 30 mm larva from BUDGETT'S collection.

The conditions seem to be practically the same in the present 24 mm specimen as in the 30 mm larva described in MOY-THOMAS'S paper. The arches are ossified to a great extent but chiefly their proximal portions.

There are only some observations concerning the development of the epibranchials of the first arches that may be considered to be of some interest, as MOY-THOMAS has not gone into details about these parts of the branchial skeleton.

In the 24 mm larva the distal end of the first branchial arch is not yet ossified (fig. 5). It turns mediad and slightly dorsad. The epibranchial is turned

rostro-ventrad and articulates against the cerato-branchial. On the anterior surface near the proximal end of the epibranchial is a deep indentation or groove for the efferent branchial arteria. The infra-pharyngo-branchial follows rostrad on the epibranchial. It is directed rostrad and mesiad and does not get into contact with the skull. There is no trace so far of any supra-pharyngo-branchial. In a 37 mm specimen (fig. 5) the epibranchial has developed a lateral process which articulates against the auditory capsule. This process is the future supra-pharyngo-branchial. The infra-pharyngo-branchial is still entirely free but is now pointing rostro-ventrad in an angle of 45°, as does the epibranchial.

In later stages the supra-pharyngo-branchial grows out still more and attains almost the length of the infra-pharyngo-branchial. Both ossifie separately while the epibranchial often remains cartilaginous even in the adult. Hence the description by ALLIS (1922) is understood where the pharyngo-branchial of the first arch (in his fig. 16) is the infra-pharyngo-branchial and what he calls the epibranchial of the first arch is the supra-pharyngo-branchial. The epibranchial is what ALLIS describes as "an independent bit of cartilage interposed between the epibranchial and ceratobranchial".

The ontogenetical development of of the supra- respectively infra-pharyngo-branchials in *Polypterus* is thus the same as in *Amia* (HOLMGREN 1943) and *Lepidosteus* (HAMMARBERG 1937).

CARTILAGE BONES.

The first ossifications in the neural cranium are the *sphenoid* and the *occipital* which are already developed in the 24 mm specimen (fig. 2). The sphenoid is formed as a perichondrial lamella in the wall of the orbita between the posterior margin of the fenestra optica and the common foramen for the nn oculomotorius and profundus. During the following stages ossification progresses very little caudad. In a 76 mm specimen (fig. 4) the posterior margin of the sphenoid surrounds the anterior half of the above-mentioned nerve foramen. Rostrad the bone has grown by means of ossification of the connective tissue membrane of the fenestra optica. This fenestra is covered with bone in the 76 mm specimen, except in the anterior part. Dorsally the margin of this membrane bone is joined to the perichondrial bone forming on the ventral edge of the taenia marginalis. Ventrally the membrane bone is free from the trabecles except at the posterior margin of the optic foramen. There is no subdivision of the bone in alisphenoid resp. orbitosphenoid elements, as already pointed out by HOLMGREN—STENSIÖ with regard to older specimens.

The *autosphenotic* appears in the 37 mm specimen (fig. 3). It fuses with

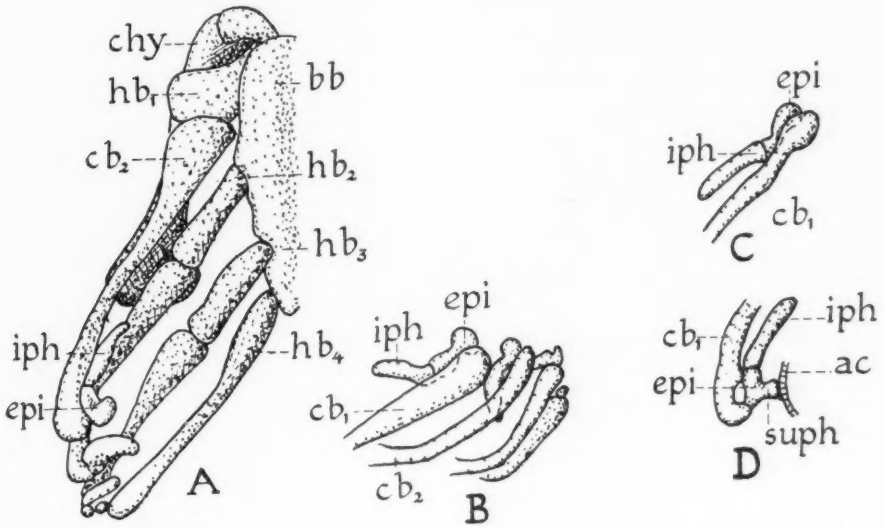

Fig. 5. *Polypterus senegalus*. Branchial skeleton in 24 mm specimen (32×1). A. in dorsal view, B. in lateral view, C. dorsal end of first branchial arch in 37 mm specimen in lateral view, D. in dorsal view (20×1).

the dermosphenotic already developed. The *ectethmoid* and the *opisthotic* are visible first in a 76 mm specimen (fig. 4).

In the 37 mm specimen a thickening of the perichondrial lamella is seen round the posterior margin of the trigeminus foramen (fig. 3). This is the position of a *prootic*. Already in slightly older specimens (45 mm and older) there is no trace of an ossification visible and in the adult there is no prootic. The transitory appearing prootic rudiment during the ontogeny may be interpreted either as the remains of an earlier existing independent bone, or, more probably the remnant of a formerly uniform ossified endocranium as in the Palaeoniscids.

Professor NILS HOLMGREN has kindly informed the author that he discovered a prootic rudiment of the same shape and in the same position in a series of a 30 mm specimen of *Polypterus lapradei* he had the opportunity of examining.

In the young larvae there are no ossifications in the Meckelian cartilage. First in the 76 mm specimen a cap-like perichondrial ossification begins to form round the anterior end of the Meckelian cartilage. It is the *mento-mandibular* bone.

The same applies to the *articular*. In a 45 mm specimen there are still no signs of this bone, but in a 76 mm specimen a perichondrial lamella has formed round the posterior end of the cartilage. Rostrad the ossification reaches as far as to the level of the fifth mandibular pore. In a 101 mm specimen ossi-

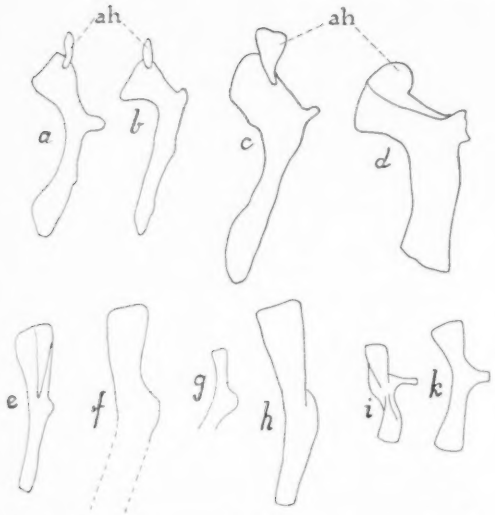

Fig. 6. Left hyomandibular bone, a—c. in *Polypterus senegalus*. a. in 24 mm specimen, b. in 37 mm, c. in 76 mm, d. in adult *Polypterus bichir* (from ALLIS), e. in *Glaucolepis magna* (from NIELSEN), f. in *Borcolepis jenseni* (from ALDINGER), g. in *Elonichthys caudalis* (from WATSON), h. in *Pygopterus nielseni* (from ALDINGER), i. in *Borcosomus arcticus* (from STENSIÖ), k. in *Acrorhabdus bertili* (from STENSIÖ).

fication has not progressed any more rostrad although the articular has formed large lamellae. The articular is everywhere separated from the angular-splenial by connective tissue.

The *hyomandibular* (hyosymplectic of some authors) is slightly falciform in young larval stages (fig. 2—4). In the adult the proximal portion is bent almost at right angles to the distal half. It seems probable from the position of the accessory hyomandibular bone (fig. 6) that the difference in shape between the larval and the adult hyomandibular is due to an actual bending of the hyomandibular bar. It has an almost vertical position in larval stages but in the adult it is more or less horizontal. This change in the shape of the hyomandibular may be due to the prolongation of the cheek region (cf. p. 411). In Palaeoniscids the cheek region has a different shape from that in *Polypterus*. The dorsal portion of the cheek is comparatively short whereas the ventral portion is elongated in a rostro-caudal direction. This circumstance seems to influence the shape of the hyomandibular as well, for the Palaeoniscid hyomandibular more closely resembles the larval hyomandibular in *Polypterus*.

In the 24 mm specimen of *Polypterus* a perichondrial ossification has already developed round the cartilage, which it covers entirely except at the dorsal and the ventral end, thus very much as is the case in the adult. The accessory hyomandibular bone has also formed as a perichondrial ossification from the dorso-caudal process of the hyomandibular bar. It has also developed the characteristic bone lamella outside the epihyal bone.

The homologues of the different bones and of the cartilage itself including the two posterior processes have been dealt with by HOLMGREN—STENSIÖ (1943, p. 94—102), whose conclusions entirely agree with the results of the present author.

If only the ossified part of the hyomandible in larval specimens of *Polypterus* is taken into consideration the resemblance to the Palaeoniscid hyomandible is

striking (fig. 6), not only as far as general shape is concerned but even regarding the posterior processes, the position of the nervus hyoideus—in some Palaeoniscid hyomandibles marked by a groove in the posterior margin above the process for the opercular cartilage—and the position of the accessory hyomandibular.

The Crossopterygian hyomandibula differs greatly from the Palaeoniscid (and *Polypterus*-) type. There is a dorsal and a ventral articulation head and the proximal portion of the bone is pierced by a canal, through which runs the canal for the hyomandibular nerve, whereas the distal portion has two lateral parallel grooves for the mandibular and the hyoid rami.

THE SENSORY LINE SYSTEM.

OL.
28
947

The sensory canal system has been described in detail by ALLIS (1900 and 1922). As typical features may be pointed out the extremely regular arrangement of neuromasts and pores, one pore always separating two neuromasts from each other; the comparatively low number of neuromasts in the canal system, not only on both sides of the same specimen, but, in every specimen examined, also, as far as the three different species examined are concerned.

The pit line system in the adult *Polypterus* has been described by ALLIS (l.c.), GERARD (1937), HOLMGREN (1942) and lately by JARVIK (1947), who, has examined a number of adult specimens and added two new lines to the ones recorded earlier. The author has discovered the same lines in the larval material independently from JARVIK.

From the conditions in the adult, as described by JARVIK, the larvae differ chiefly in the comparatively low number of sense organs in the various lines. The pit line in the snout, for instance, has more than 20 sense organs in the adult, according to JARVIK. In the 24 mm specimen there are only six on each side, and in the 37 mm specimen seven (fig. 7).

The line on the snout is probably identical with the line described by the author in *Gymnarchus* (PEHRSON 1945), and there called the nasal line. It is called the tectal line by JARVIK (cf. p. 429 in this paper). In *Polypterus* as in *Gymnarchus* it is innervated by the nervus ophtalmicus superficialis (figs. 7 and 8), according to the author's observations. The writer suggested (1945) that the nasal pit line in *Gymnarchus* was the product of a differentiation of the nasal portion of the supraorbital sensory line, a suggestion founded on the ontogeny of an infraorbital line of pits in *Esox* (PEHRSON 1944). Although the innervation may speak for a similar explanation in *Polypterus* the problem is more difficult to solve definitely because the supraorbital canal in the 24 mm specimen is already formed, with exception of the portion that later will be situated in the so-called terminal bone. This part of the canal is only to be

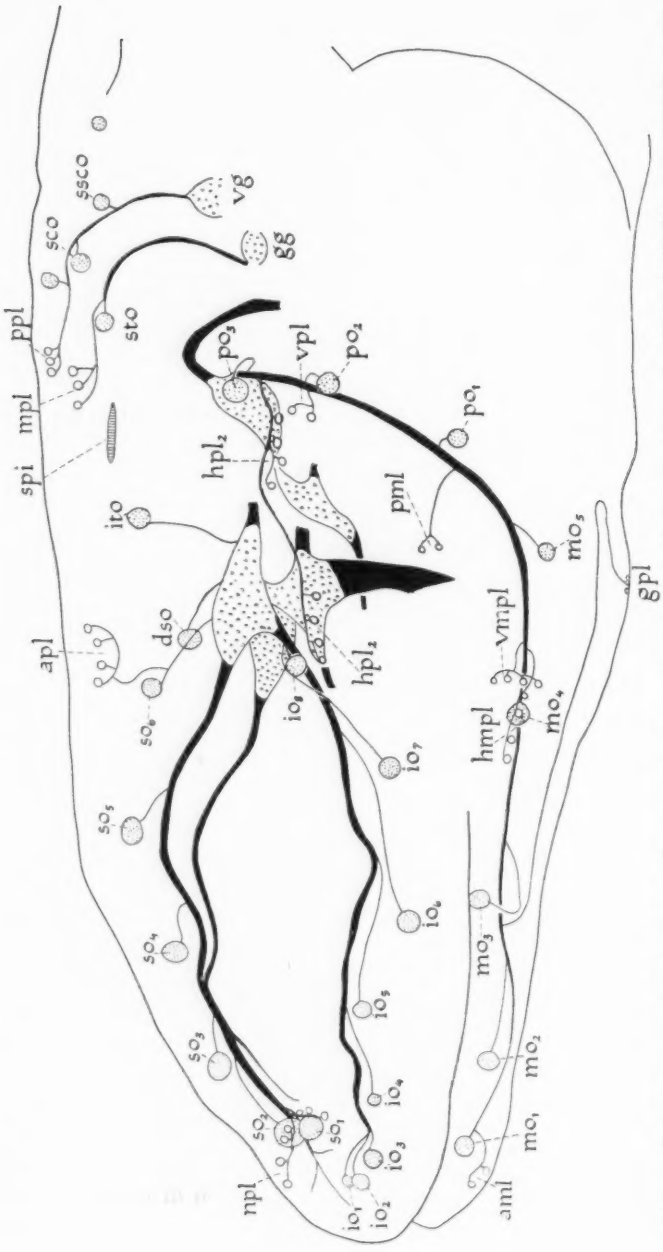

Fig. 7. *Polypterus senegalus*, 37 mm. Innervation of neuromasts and pit line sense organs. Dotted circles, neuromasts, open circles, pit line sense organs (31×1).

seen as an insignificant groove in the epithelium. The neuromast that belongs to the future canal is lying superficially and differs only in its size from the sense organs of the pit line. Possibly the examination of still earlier stages may provide material for an understanding of the ontogeny of the nasal line.

The so-called anterior pit line of the head in the adult consists, according to JARVIK, of 4—7 sense organs. In a 24 mm specimen there are only two organs developed (fig. 17). At this stage the line has a slightly different position than in the adult. All records on the position of this line in the adult agree that it occupies an oblique position with the antero-lateral end close to the fifth pore of the supraorbital canal. In one of JARVIK's specimens it is even placed still further back. In this young larval specimen the more antero-lateral of the two organs is placed immediately postero-medial to the fifth neuromast in the supra-orbital line which is the most caudal organ in the frontal canal which indicates a movement rostrad during the later ontogeny. The second organ, besides, lies directly caudad to the first organ, the two organs forming a short longitudinal line.

JARVIK's opinion is that the position of this line has a certain importance as it should recall the situation of the line in Osteolepiform Crossopterygians, whereas in Palaeoniscids a longitudinal groove is interpreted as this line. The present writer does not attach too much importance to the question of the line's position, yet, it might be mentioned that the position of the line in the young larvae actually seems to point to Palaeoniscid conditions rather than to Crossopterygian. It has almost exactly the same position in a 37 mm specimen as in the 24 mm specimen.

The line is innervated by the same branch of the facialis as the 6th supraorbital neuromast (fig. 7). This nerve does not branch of from the ophtalmicus superficialis, but leaves the ganglion between the root of this nerve and the "dermosphenotic" branch. Four separate nerves take their origin from the dorsal portion of the ganglion, most rostrally the ophthalmicus superficialis, next to it the above mentioned nerve, further back the "dermosphenotic" nerve, and most caudally the otic nerve (fig. 7).

The middle and the posterior pit lines form, apparently, one transverse line in the 24 mm specimen (fig. 17), formed by three sense organs. As in the adult the line extends laterally to the 10th pore of the infraorbital canal. In the 37 mm specimen the line is divided in two portions with three organs in each, and forming an angle (fig. 7). HOLMGREN (1942) has pointed out that the medial division of the line is to be interpreted as the posterior pit line, whereas the lateral portion is the middle head line of pits. His opinion is now confirmed by the fact that the lateral division is innervated by the same branch of the glossopharyngeal nerve as the supratemporal neuromast. The medial division, that is to say, the posterior line of pits is ennervated from the same branch of the vagus as the neuromasts of the supratemporal canal commissure.

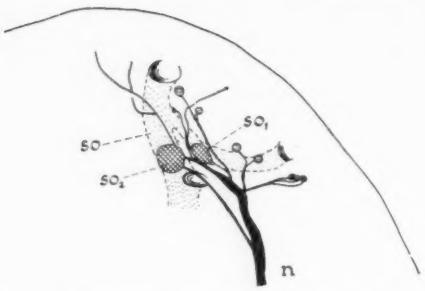

Fig. 8. *Polypterus senegalus*, 45 mm. Innervation of supraorbital neuromasts No. 1 and No. 2, and of sense organs in nasal pit line (32×1). Circles with crossing lines, neuromasts, small circles with horizontal lines, pit line sense organs. Profundus branches of the mixed nerve (*n*) visible rostrally and rostrolaterally.

Under such circumstances, it is difficult to follow JARVIK who doubts HOLMGREN'S interpretation. Instead he tries to explain the two divisions as corresponding, the lateral portion to the supratemporal pit line and the medial to the transverse parietal pit line in Crossopterygians. Nothing is known concerning the innervation of these lines in the Crossopterygians. It seems far more probable that the transverse parietal and the supratemporal lines in Crossopterygians correspond to the middle head line in Actinopterygians, while the posterior oblique line in the Crossopterygians is the homologue of the posterior head line in the Actinopterygians.

The horizontal pit line of the cheek consists in the young larvae of two different portions, one anterior and one posterior (figs. 7 and 16). The anterior line begins immediately caudally to the 7th pore of the infraorbital canal. In the 24 mm specimen this pore is, so far, only represented by its dorsal half, as the ventral portion of the canal is not yet formed. In the 37 mm specimen, where the canal system is entirely formed, the line consists of four sense organs. In older stages this part of the line will be situated outside the dorsal margin of the caudal end of the "maxillary". The posterior portion has its posterior end immediately rostrodorsally of the 8th pore in the preoperculomandibular canal. It also consists of four sense organs in the 37 mm specimen. Both lines are innervated by the same branch from the nervus hyoideomandibularis, which leaves the nerve trunk near the exit for the 8:th and most dorsal preopercular neuromast (fig. 7).

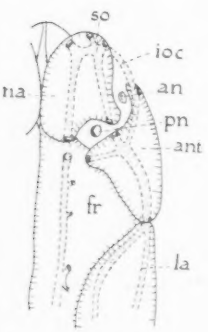

Fig. 9. *Lepidosteus osseus*. Sensory canals in the snout (after ALLIS).

In adult specimens this line consists, according to JARVIK, of four distinctly separate portions. In the oldest of the specimens available for the present investigation, an 125 mm specimen of *Polypterus bichir*, there are still only two lines visible. Now the cheek of a young *Polypterus* is very short, compared to the unusual length of this portion of the head in an adult animal.

In order to state exactly the difference in relative growth in length of the different parts of the head in Polypterus senegalus the following measurements were made: (a) the distance between the tip of the nose and

the anterior margin of the eye, (b) the distance between this point and the vertical tangent of the infraorbital sensory canal behind the eye, (c) the distance between this point and the vertical tangent of the preopercular canal, (d) the distance between this point and the vertical tangent of the most posterior point of the operculum. The measurements were made (1) in the 24 mm specimen, (2) in the 37 mm specimen, (3) in four adult specimens (the average figures were used). In the table below the length of the different regions of the head is given as a percentage of the total length of the head.

	1	2	3
a	19.3	18.8	18.6
b	26.4	24.3	15.1
c	20.7	22.2	29.7
d	33.6	37.7	36.6
	100	100	100

VOL. 28 1947

The table shows that whereas the snout (a) has practically the same relative length in the three stages, the relative length of the eye-region (b) diminishes, while the cheek-region (c) increases considerably. The opercular region (d) also takes proportionally a larger part of the head in the adult than in the larva.

It is therefore possible that JARVIK's four separate portions of the line are the result of the great increase in length of the cheek part during the later ontogeny. This is made still more probable because the third part in JARVIK's description has been observed only in one specimen. This line consists of two elements also in *Glaucolepis* (fig. 27).

The vertical pit line of the cheek is situated immediately in front of the preopercular canal (figs. 7 and 16). At the larval stages it consists only of two organs innervated by a little nerve, which branches off from the nerve supplying the 7th preoperculo-mandibular neuromast.

On the cheek of *Polypterus* there is still another line described by HOLMGREN (1942) and called by him the primary mandibular line. JARVIK calls it the quadrato-jugal pit line (figs. 7 and 16). It is formed in the larvae by two organs only, but has in the adult, according to JARVIK, from 2 to 12 organs. In the adult it is situated near the Traquair bones *y* which are not developed in the young larvae (cf. p. 436).

There are three different lines in connection with the mandibular sensory canal. Most rostrally is the short anterior mandibular line. It is innervated by a branch from the ramus mandibularis, the branch leaving posterior to the first mandibular organ (fig. 7). It is no doubt homologous to the same line described by the author in *Gymnarchus* (PEHRSON 1945). HOLMGREN (1942) calls it an anterior gular line. The original (posterior) gular line in *Polypterus* is innervated by a branch from the ramus mandibularis, but, this branch runs in a

long loop caudad before it joins the nerve (fig. 7). The gular nerve runs in a similar loop as well in *Amia*. The organs in the the anterior mandibular line on the other hand are innervated by a nerve which branches off close to a group of sense organs. If this circumstance has any importance it seems less probable that it is a question here of a gular line.

Dorsally to the mandibular canal at the same height as the 4th mandibular neuromast is a short horizontal line, innervated by a nerve branching off from the ramus mandibularis, posterior to the 4th neuromast (fig. 7). It is the line HOLMGREN calls the mandibular pit line.

Immediately posterior to this longitudinal line is another short line, though, with a transverse position. It is innervated the same as the longitudinal line, the only difference being that the nerve branches off a little more posteriorly (fig. 7). This line is not mentioned by HOLMGREN (1942). According to JARVIK it may sometimes be doubled.

The three lines connected with the mandibular line are called by JARVIK different portions of the mandibular line, viz. the anterior transverse, the longitudinal and the posterior transverse portions. JARVIK considers that "as the squamosal pit line in Osteolepids is often continous with the quadrato-jugal pit line and as the quadrato-jugal in *Holoptychius* is clearly continued by the mandibular pit line" the vertical, quadrato-jugal and mandibular pit lines in *Polypterus* form parts of the same sensory line. That may be so, but, the argumentation sounds unconvincing and is in any case insufficient.

To the pit lines now enumerated, may be added the gular line. It differs only in its shortness from the conditions in the adult. The innervation of this line is mentioned above (fig. 7).

In the 24 mm larva the sensory canal system is formed, except in some parts. The supraorbital line is entirely developed with the exception of the canal in the terminal bone (cf. p. 409 and p. 426 in this paper).

The rostral commissure is also developed. As to the infraorbital line, the portion of the canal is closed where the first five organs are lodged, but, the sixth organs is still lying at the bottom of a groove. The canal is formed as far caudad as to the fifth pore where it ends with the rostral rim of the pore. There is no indication in the skin of the future canal between this point and the groove where the 6th neuromast is situated. The same condition applies to the portion between the fifth and the sixth pore. Only the proximal (dorsal) lip of this pore is formed as it marks the entrance to the next portion of the canal. Hence there is an open space between the lip of the sixth pore and the sixth neuromast. The postorbital portion of the canal is formed.

There is an open space between the pores Nos. 6 and 7 in the preopercular canal. The neuromast No. 6 is thus lying quite open in the skin, and not even an indication of a groove is seen.

The main canal ends with the pore posterior to the supratemporal neuromast.

VOL
28
194

No trace of a supratemporal canal commissure is formed, and the neuromasts are lying superficially in the skin.

The infraorbital canal is already entirely closed in a 29 mm specimen, but, the gap between the neuromasts Nos. 5 and 6 in the preoperculo-mandibular line, thus, between the mandibular and the preopercular portions of the canal is not closed until the 37 mm specimen.

THE SENSORY CANAL PATTERN IN POLYPTERUS, HOLOSTEANS AND PALAEONISCIDS.

JARVIK recently (1942) pointed out that what has been considered as the rostral part of the supraorbital sensory line in *Palaeonisciformes,* Saurichthyids and sturgeons cannot possibly be the homologue of the anterior portion of the supraorbital canal in *Polypterus,* Coelacanthids and Rhipidistid Crossopterygians (JARVIK, l.c., p. 616). Furthermore he gives a partly new interpretation of the sensory canals and dermal bones in the snout of Actinopterygians (l.c., p. 617—619).

To this end he claims the existence in Crossopterygians and Actinopterygians (including *Polypterus*) of two transverse commissures between the supraorbital and the infraorbital canals, an anterior commissure and a posterior. It will be necessary to make his exposition the subject of a rather detailed scrutiny. His views on the two commissures are chiefly founded on studies of the works of ALLIS and the present author as well as on reinterpretations of results gained by NIELSEN (1936) and STENSIÖ (1932).

ALLIS, in his description of the lateral line system in *Amia* (1889), mentions an "antorbital cross-commissure" and describes it in this way (p. 471): "This antorbital portion which is more properly an anterior cross-commissure connecting the two main infra-orbital lines, seems to be found in some other ganoids; for TRAQUAIR describes a similar connection in *Polypterus bichir,* and LEYDIG three of them in *Chimaera monstrosa*; but it is not found in the *teleostei,* so far as can be judged from the descriptions I have been able to find." This so-called anterior cross-commissure is, thus, nothing but what is termed more commonly the ethmoidal or rostral cross-commissure. It has nothing to do with JARVIK's alleged "anterior cross-commissure".

ALLIS continues (p. 471): "The suborbital part of the infra-orbital part is, in the adult, connected at its anterior end, immediately in front of the posterior nasal aperture, with the supra-orbital canal. There is no direct union of the two lines here, the connection being of the nature of a commissure formed by the anastomosis of the two dendritic systems, one of which is the terminal system of the suborbital, and the other the fourth regular system of the supra-orbital canal." This is obviously the "posterior transverse commissure" which

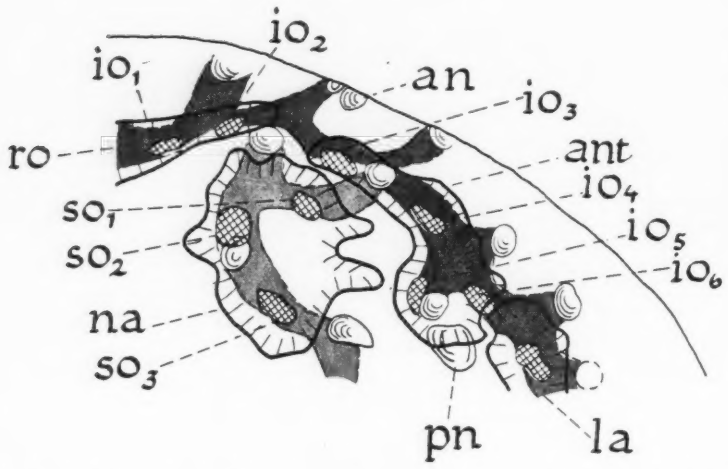

Fig. 10. *Amia calva*, 22 mm. Sensory canals and canal bones in the snout, dorsal view. Crossed lines, neuromasts. Light shade, supraorbital sensory canal, dark shade, infra-orbital (28×1).

plays such an important part in JARVIK's discussion of the morphological conditions in the snout of fishes.

ALLIS continues, however, (p. 475) concerning the trunk of the 6th peripheral dendritic system of the infraorbital line, which trunk issues from the posterior edge of the antorbital: "Trunk 6 is a direct continuation upward and backward of the antorbital part of the main canal, and is comparatively long, extending from the bend in the canal to a point beyond the upper posterior margin of the bone and a little in front of the posterior nasal aperture. Here it runs directly into, and is continous with, trunk 4 supraorbital, the two trunks or some of their branches meeting and anastomosing, and so forming a direct connection between the two canals. — — —"

"The anastomosis of these two peripheral systems is not formed until the fish is well advanced in age. In the large 15-month specimen shown in (ALLIS's) fig 17 it is just forming. It is brought about in the following way: trunk 4 supra- orbital, which leaves its canal immediately in front of the frontal, runs forward and laterad until it reaches a point median to the anterior edge of the posterior nasal aparature. Here it turns backward, and runs toward the anterior edge of the frontal, often extending beyond this edge onto the upper surface of the bone. Trunk 6, infra-orbital, lies almost exactly in the line of the main part of trunk 4, supra-orbital, the two trunks and their system of pores and branches growing directly toward each other until either the trunks or some of their branches come squarely together and unite at or near the bend in trunk 4, enlargements being usually formed at the points of union. A remnant of the dividing wall remains, indicating the line where the two systems came together.

This is the only place in the entire lateral system of Amia where an anastomosis below the surface occurs." (italics by E. Ph. A.)

From ALLIS's description is evident 1) that there is no "anterior transverse commissure" between the infraorbital and the supraorbital lines, 2) that the so-called "posterior transverse commissure" is only a secondary union between the tubes of the two adjacent canals, a union that occurs very late and is brought about either by the trunks of the pore canals or by their branches. It is obvious that such a connection has no wider morphological value and under no circumstances can be used for the establishing of far reaching morphological conclusions.

JARVIK tries, in addition to get support for his opinion in two papers on the development of the dermal skull in *Amia* by the present author (PEHRSON 1922 and 1940), where he refers to not less than nine figures. It may be pointed out that the author himself is perfectly unaware of the existence of the "cross commissures" in spite of meticulous researches.

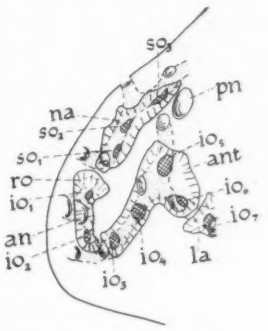

Fig. 11. *Amia calva*, 22 mm. Same as in fig. 10, lateral view.

The anterior of these supposed commissures is according to JARVIK only vestigial "being represented by the foremost laterally bent portion of the supraorbital sensory canal that lies close behind the anterior external nostril in the antero-lateral part of the so-called nasal and lodges organ 1 of the supraorbital sensory canal." It is obvious that JARVIK speaks of a different "commissure" from ALLIS in the paragraph quoted above, the "commissure" in ALLIS's sense being the ethmoidal cross-commissure, whereas JARVIK refers to the distal end of the sensory canal in the nasal bone. The alleged posterior commisure on the other hand is identical with the anastomosis in the dendritical pore system as, according to JARVIK, the ventral part of the commissure is situated "in the postero-dorsal part of the so-called antorbital and lodges organ 5 of the infraorbital sensory canal".

It may briefly be stated that there is no "anterior commissure" either in the adult *Amia* or in any period during the development of the sensory canal system in that fish. At young stages there is a very pronounced lateral bending of the distal portion of the supraorbital sensory canal (fig. 11) but there is never any indication of any junction between the end of this canal and the infraorbital canal.

JARVIK attaches so much importance to these transverse commissures—they are fundamental for his interpretations of the homologies of the dermal bones in the snout of fish—that it might be of a certain interest to investigate their occurrence in the other cases referred to by him.

As to *Polypterus*, JARVIK (1942, p. 618) asserts the "presence in *Polypterus*

of an anterior transverse commissure". In another page (l.c., p. 602) the following statement is found: "Immediately behind its anastomosis with the infraorbital canal in *Polypterus* it [the supraorbital canal] gives off a postero-ventro-lateral branch situated immediately behind the proximal part of the anterior external nasal tube. The position and course of this branch, which is currently regarded as the foremost end of the supraorbital sensory canal, reminds considerably of the anterior transverse commissure in Coelacanthids." The part of the canal referred to is the one lodged in the so-called os terminale (nasale I, HOLMGREN—STENSIÖ 1936). It corresponds in position at least in larval specimens almost exactly to the laterally bent portion of the foremost end of the supraorbital canal in *Amia* mentioned above (cf. p. 429 in this paper). JARVIK explains further (1947): "the canal in the terminal is probably not the anterior part of the supraorbital sensory canal, but represents a vestige of the anterior transverse commissure between the supraorbital and infraorbital canals, which is completely developed in certain Coelacanthids and Actinopterygians (e.g. in *Sinamia*)".

It will be necessary to follow JARVIK's explanations concerning the supposed commissures in fossil fishes as well. In *Eusthenopteron foordi*, JARVIK (1944) has found that "the tubes of the infraorbital and supraorbital canals that enter the supraorbito-tectal may anastomose with one another, thus connecting the said canals. In certain specimens a real canal may also be developed between the supraorbital and infraorbital canals at this place." This connection is not formed in the place for the "anterior commissure" referred to above (JARVIK 1942, fig. 17) nor for the "posterior commissure" and occurs only in some specimens. Besides it is caused by anastomosis between the largely branching and spreading tubes, not by connection between the canals. It cannot be used as any kind of evidence in the present discussion.

Amongst the Crossopterygians JARVIK ascribes the transverse commissures to the Coelacanthids. This is the evidence he presents:

In the two Devonian Coelacanthids *Nesides* and *Diplocercides* described by STENSIÖ (1937) there is in the lateral rostral a foramen through which the infraorbital sensory canal opens in a dorsal direction. This foramen which was overlooked by STENSIÖ according to JARVIK, lies in the place corresponding to the one in NIELSEN's undetermined Coelacanthid (NIELSEN 1936; cf. p. 417 in this paper) where the lateral rostral is pierced by the supposed posterior transverse commissure. JARVIK continues: "Judging from its position, the foramen must thus have given passage either to a corresponding commissure or to a large tube representing this commissure in an initial stage of development." Unfortunately the dermal bones of the posterior portion of the ethmoidal region in the specimens of both Nesides and Diplocercides are deficient. The supraorbital sensory canal is further only known by its pores. JARVIK admits that "it cannot for the present be decided which of the said two alternatives is true".

VOL
28
194

In the two other known Devonian Coelacanthids *Euporosteus* and *Dictyonosteus,* in which the supraorbital canal is known, there is no indication of any transverse commissures.

As mentioned above, NIELSEN (1936) has described an undetermined Triassic Coelacanthid from Spitzbergen. JARVIK has reinterpreted NIELSEN's results and ascribes to this Coelacanthid a posterior transverse commissure between the supra- and the infraorbital canals. From this commissure runs, according to JARVIK, a longitudinal commissure, by NIELSEN interpreted as a part of the infraorbital canal. Anteriorly this supposed longitudinal commissure sends out a long tube in the shape of a ventrally directed branch (according to NIELSEN's description), although emanating from the ethmoidal commissure of the infraorbital canal. This tube does not reach what is supposed to be the infraorbital canal in JARVIK's interpretation. Although it is not connected with the so-called infraorbital canal JARVIK considers it as representing the "anterior transverse commissure". In this Triassic form, thus, there is a—supposed—anterior transverse commissure and a—still incomplete as the latero-ventral portion is missing—posterior transverse commissure.

There remains so far one more Coelacanthid to be considered, viz. *Latimeria.* There JARVIK reinterpretes SMITH's description (1940) and forms a pattern of sensory canals in the snout, much resembling the result of his reinterpretation of the canals in NIELSEN's undetermined Triassic specimen. But JARVIK admits that SMITH was unable to trace with certainty the course of the sensory canals in the snout of *Latimeria.*

This is the evidence collected from the Coelacanthid material to which JARVIK refers in his paper.

As to *Polypterus* he points out (p. 602) that the position of the foremost end of the supraorbital canal which lodges organ No. 1 and is enclosed in the so-called os terminale (or nasal 1, cf. p. 407 and 426 in this paper) "reminds considerably of the anterior transverse commissure in Coelacanthids". Without regard to the fact that these commissures are dubitable, to say the least, in Coelacanthids, and that there is no "commissure" in *Polypterus,* as the ventrolateral part is missing, JARVIK refers (p. 618) to "the presence in *Polypterus* of an anterior transverse commissure apparently homologous to that in Coelacanthids."

JARVIK also states in his paper that his analysis of the sensory canals may throw some light on the conditions in *Palaeonisciformes* and writes: "It is thus not difficult to see that the ventro-laterally running preorbital portion of the supraorbital sensory canal in *Palaeonisciformes* in its lower part, situated behind the fenestra exonarina anterior, is essentially as the anterior transverse commissure between the infraorbital and supraorbital canal in *Amia, Sinamia, Polypterus* and *Coelacanthoidea.*"

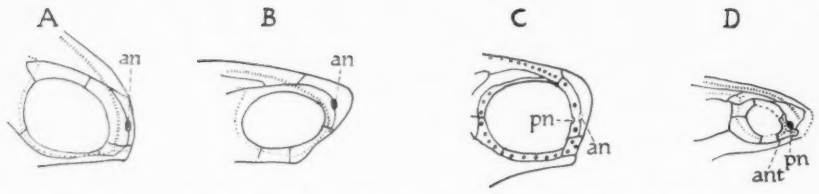

Fig. 12. Four Carboniferous Palaeoniscids. A. *Canobius ramsayi* (after MOY-THOMAS and DYNE). B. *Cycloptygius concentricus* (after MOY-THOMAS and DYNE). C. *Cornuboniscus budensis* (from WHITE). D. *Coccocephalus Wildi* (after WATSON). Line of dots, infraorbital sensory canal, line of short transverse strokes, supraorbital sensory canal.

JARVIK refers for proof to a figure showing the snout in *Canobius ramsayi* and *Cornuboniscus budensis* (fig. 12 in this paper). Further he claims to have seen a posterior transverse commissure "at least in certain *Palaeonisciformes* such as *Cheirolepis* and *Birgeria*" (fig. 14 in this paper). As to *Canobius* and *Cornuboniscus*, they will be discussed later in this paper (p. 424). Concerning the anterior end of the supraorbital canal in *Cheirolepis*, WATSON (1925) writes that its character is unknown "but it presumably becomes continous with an ethmoidal cross-commissure". He admits that "it is unfortunate that the relations of this commissure to the infra- and supraorbital canals remain unknown".

In *Birgeria* (STENSIÖ 1932, fig. 41) "the commissure ascends in a dorsal process from the posterior part of the bone that STENSIÖ has termed 'antorbital'" (quoted from JARVIK). This ascending branch from the infraorbital canal is quite correctly declared by JARVIK to be the homologue of the dorsal canal branch in the antorbital in *Amia*, but, just as in *Amia* there is no "commissure" to be found.

The pattern of the canals in the snout in these fishes will be discussed later in this paper (p. 423).

STENSIÖ (1935) has described the sensory canal system in *Sinamia*. The anterior portion of the supraorbital canal enters the nasal in the postero-medial corner, runs almost straight rostrad and bends near the anterior rim of the nasal laterad and continues in a caudo-lateral direction. According to STENSIÖ, it anastomoses there with the part of the infraorbital canal situated in the antorbital. This anastomosis is the anterior transverse commissure in JARVIK's sense.

Fig. 13. Two Permian Palaeoniscids. A. *Brachydegma caelatum* (after DUNKLE). B. *Palaeoniscus freislebeni* (after ALDINGER). Line of dots, infraorbital sensory line. Line of short transverse strokes, supraorbital sensory line.

The infraorbital canal runs rostrad through a series of infraorbital bones and then passes into the antorbital. In this bone it makes a curve dorsad where it forms a dorso-mediad directed branch. The rest of the canal continues rostrad

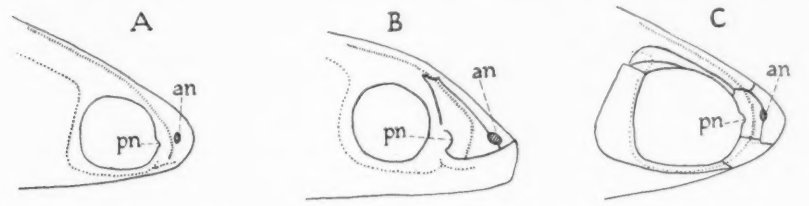

Fig. 14. Three Triassic Palaeoniscids. A. *Glaucolepis stensiöi* (after NIELSEN). B. *Birgeria groenlandica* (after STENSIÖ). C. *Boreosomus piveteaui* (after NIELSEN).

and meets its vis-à-vis from the other side and forms the supraethmoidal commissure. The medio-dorsal branch in the antorbital is supposed to anastomose with the supraorbital canal after having passed anterior to the posterior nasal opening. This anastomosis corresponds to JARVIK's posterior transverse commissure. Thus, at least, is the representation of the sensory canal system in figs. 18 and 19 in STENSIÖ's paper. In his description he writes (p. 34) concerning the first mentioned commissure that it is "likely" that the portion of the infraorbital canal in the antorbital which runs straight rostrad towards the anterior margin of the bone anastomosed with the anterior end of the supraorbital canal in the nasal. Concerning the dorsal branch of the canal in the antorbital, STENSIÖ says that it "probably anastomosed with the supraorbital canal". It should then represent the post-nasal commissure in *Amia* (cfr. p. 415 in this paper).

JARVIK in his paper when referring to *Sinamia* has omitted the "likely" and "probably" and states: "In the fossil Amiid *Sinamia* there are between the anterior and posterior external nostrils two transverse commissural canals, anterior and posterior, connecting the supraorbital and infraorbital canals" (p. 617).

It seems most "likely" that the "anterior commissure" is no commissure at all, at least from what can be seen in STENSIÖ's plate I, where in the left side the canals are clearly seen. As in *Amia* the sensory canal in the nasal makes a sharp bend laterad and then continues caudad as in *Lepidosteus* (figs. 9 and 15). No anastomosis can be traced, however. As to the infraorbital canal, a

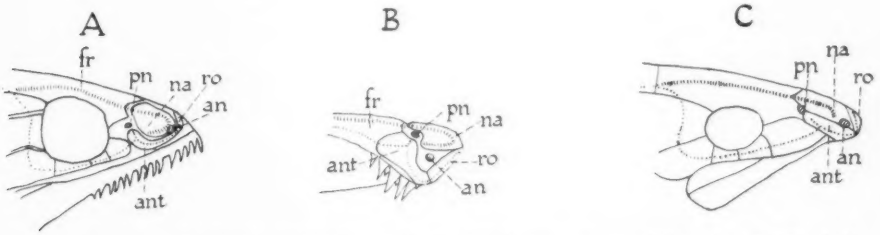

Fig. 15. A. *Sinamia zdanski* (after STENSIÖ). B. *Lepidosteus osseus* (after ALLIS). C. *Amia calva* (after ALLIS).

short piece of the canal is visible on the left side in the first infraorbital bone. There is a three-branched portion of the canal in the antorbital. The anterior branch continues rostrad as the ethmoidal commissure. The posterior branch is broken off at the posterior margin of the bone but has its continuation caudad in the first infraorbital. As to the third or dorsal branch it divides near the medial margin of the bone into two short canals. No anastomosis with the supraorbital canal is to be seen. It may be suggested that this short dorsal branch, which according to STENSIÖ "probably anastomosed with the supraorbital canal", simply represents a dorsally directed portion of the canal in the antorbital, and that the two short branches at the medial end of this portion form the trunk of a branching tubule. This portion should thus end with a pore exactly as is the case in *Amia*. The remains of the canal system on the right side are more imperfectly preserved. There is practically nothing of the canal in the nasal left, but, the shape of the canal in the antorbital at least does not contradict an interpretation such as the one developed now.

VOL
28
194

This suggestion also agrees with the conditions met with on the right side of the same specimen as represented in plate V where the head is seen from the right side. In the antorbital only the dorsal branch of the canal is seen, thus, the trunk of the branching tubule.

This specimen may be compared to No. 4, represented in plates XII and XIII. There the bones on the left side of the head are shown from the medial side, thus preserved as impressions. In the nasal bone the medial part of the canal is fairly well preserved with two branching tubules visible.

The antorbital is seen with a branching portion of the canal immediately caudally to the nasal. If specimen No. 4 (in plate XIII) is compared with specimen No. 2 (in plate V), the difference in the position of the antorbital in the two cases is striking. As a matter of fact the conditions in specimen No. 4 give a strong impression that the antorbital is dislocated, having been pushed from its original position in a rostro-lateral direction. In a dorso-caudal direction there is a gap in the specimen of the same shape as the bone fragment denoted as the antorbital. If the antorbital could be pushed dorso-caudad to fill up the empty space the position of the canal would be different. The ventral portion of the canal would then fit in between the anterior and posterior stumps of the infraorbital canal and the dorsal branch would be situated as a dorsal tubule, as is described above with regard to specimen No. 2. There is a short branch directed latero-caudad in the posterior portion of the part of the infraorbital canal situated anteriorly to the antorbital bone in No. 4. This little branch might be a ventral tube of the infraorbital canal. An attempt has been made to reconstruct the snout of Sinamia according to the suggestions made above (fig. 15).

What is gained is that a perfect similarity between the conditions in the snout of *Amia* and *Sinamia* will be established. There will not be any necessity

for supposing a commissure that cannot be said to exist with certainty in any other fish.

In *Lepidosteus* (figs. 9 and 15), a kind of connection is found between the infraorbital canal in the antorbital bone and the supraorbital canal. This connection—if it really should be called so—is brought forth in the way that the infraorbital canal in the antorbital bone sends a tube mesiad as in *Amia*. This tube ends in the larval specimens with a pore situated on the antero-medial edge of the bone. This bone is separated from the anterior end of the frontal by a narrow strip of tissue where the adjacent bones do not meet. The first pore in the supraorbital portion in the frontal opens opposite the pore in the antorbital. In a 70 mm specimen of *Lepidosteus* the antorbital is developed round the canal, but the anterior end of the frontal portion of the supraorbital canal is still gutter-shaped. The pore at the medial end of the canal in the antorbital opens immediately behind the posterior nasal opening. In *Amia* the corresponding pore is situated close to the rostral margin of the posterior nasal opening.

VOL. 28 1947

ALLIS (1904) states that in the antorbital, latero-postero-ventral to the posterior nasal aperture, the ethmoidal canal anastomoses, apparently by its terminal tube, with the penultimate tube of the suborbital part of the main infraorbital canal, but, as this connection does not exist in the larva and is established only by means of the pores, no morphologically real connection can be said to exist in Lepidosteus.

Current representations in the literature of the snout in *Palaeonisciformes* show a remarkable difference in the course of what is generally called the foremost part of the supraorbital canal, as already pointed out by ALLIS (1904). Seemingly the rostral portion of the supraorbital canal runs laterally to the nostril to join the infraorbital canal in the ethmoidal commissure instead of medially.

Now, there are few instances where the sensory canals in the snout of *Palaeonisciformes* are kept intact. In *Boreolepis*, for instance, (ALDINGER 1937, fig. 33, pl. 30) the supraorbital canal is seen. It traverses the parietal where the canal ends caudad and continues rostrad through the frontal but never reaches the anterior margin of this bone. No traces of an infraorbital canal are retained. In *Palaeoniscus freislebeni* (ALDINGER 1937, fig. 25, pl. 25, fig. 13 in this paper) the infraorbital canal is comparatively well preserved, but, unfortunately in a young specimen, not possible to determine with certainty. The canal traverses the bone called infraorbital where it sends one branch rostrad, the ethmoidal cross commissure. The rest of the canal turns dorsad and ends with the margin of the bone. There is nothing to be seen of any continuation of the canal dorsad or of the supraorbital canal. In ALDINGER's text figure the canal is seen running through the so-called antorbital bone (probably the nasal) and the frontal as a continuation of the supraorbital canal.

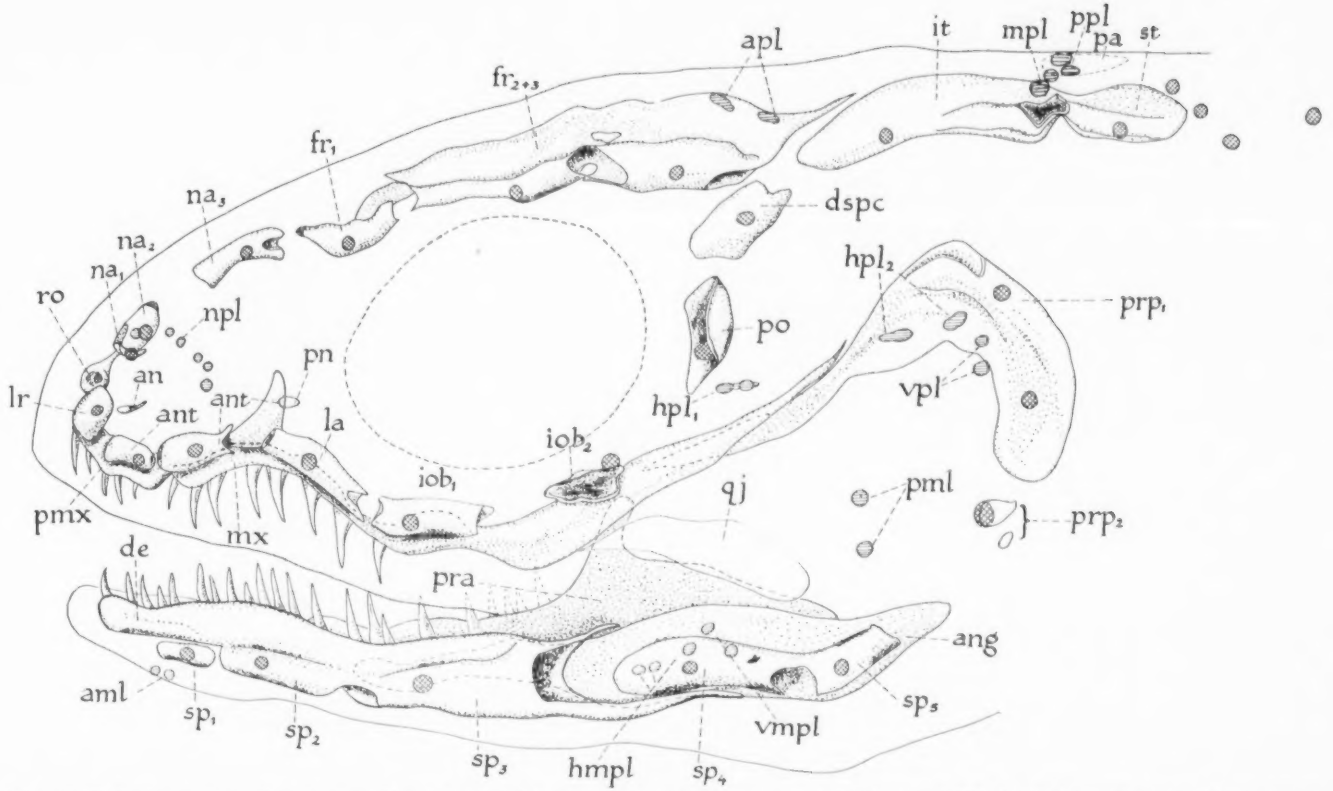

Fig. 16. *Polypterus senegalus*, 24 mm. Cranial dermal bones and sensory organs in lateral view (48×1). Circles with crossed lines, neuromasts, circles with horizontal lines, pit line organs.

VOL
28
194

This text figure is taken from WESTOLL (1935—36) and represents a reconstruction.

In *Coccocephalus wildi* (WATSON 1925) the infraorbital canal (fig. 12) enters the "lacrymal" (probably the antorbital) where it branches and sends one canal mediad, the ethmoidal cross-commissure, and one dorsad where it ends without joining the supraorbital canal which continues further rostrad than the canal in the "lacrymal" (antorbital) and runs medially to this bone in the so-called antorbital (nasal). The nasal opening is situated in the ventrolateral margin of the "antorbital" where it makes an indentation between this bone and the "lacrymal".

ALLIS (1904) suggests when pointing out the extraordinary course of the supraorbital canal in *Nematoptychius*, where the anterior part is situated in the so-called prefrontal and lies lateral to the nasal aperture, a position unknown in living fishes, as the only possibility of establishing a reasonable homology "that the so-called prefrontal is an antorbital bone, similar to that bone in *Lepidosteus*, and that the canal it lodges is the upper anterior end of the suborbital part of the main infraorbital canal, and not the anterior end of the main supraorbital canal".

To this may be added that no connection with the ethmoidal cross-commissure is shown in the figure (TRAQUAIR 1877) referred to by ALLIS.

A similar view was also held by STENSIÖ (1921, p. 246) who referred to the conditions in "the closely related Catopterids where the infraorbital canal branches in the so-called rostral and sends one branch dorsad through the antorbital lateral to the nasal openings and another mediad forming the rostral cross-commissure". According to STENSIÖ the supraorbital line ran into the infraorbital branch in the antorbital bone. The figures show the canals only represented as dotted lines. STENSIÖ suggested that the supraorbital canal would have continued forwards as a pit line over the posterior part of the nasalo-postrostral.

STENSIÖ does not maintain the opinion referred to above in a later work (STENSIÖ 1932). Discussing the course of the sensory canals in the snout portion of *Birgeria* (l.c., p. 116), he points out that the so-called antorbital should rather be considered as a nasal than an antorbital because of the indications of an anterior and a posterior nostril. The canal portion in this bone should under such circumstances be considered as belonging to the supraorbital canal and the abnormal position of this part of the supraorbital canal in the majority of the Palaeoniscids only be apparent and due to a reduction of the posterior external nasal aperture.

This canal portion shows no connection with the infraorbital canal as it ends with the ventral margin of the nasal bone. The short dorsally directed branch of the infraorbital canal in the antorbital bone (cf. p. 432) recalls the conditions in *Coccocephalus* (WATSON 1925). Also in *Brachydegma caelatum* (DUNKLE

1939) there is as in *Birgeria* a short caudo-dorsally directed branch of the infraorbital canal in the most anterior infraorbital bone (fig. 13). Owing to the poor preservation of the dorsal part of the snout, nothing can be said concerning the course of the supraorbital canal in this region in *Brachydegma*.

Cornuboniscus budensis (WHITE 1939) and *Borcosomus piveteaui* (NIELSEN 1942) belong to the few *Palaeonisciformes* where the canal system in the snout is not represented in the descriptions by dotted lines only, but, where the course of the canals may be followed by means of the pores (figs. 12 and 14). The conditions in these fishes suggest the following attempt to bring the canal system in the snout of Actinopterygians (including Brachiopterygians) into a common scheme.

In *Amia* (ALLIS 1889, PEHRSON 1922, 1940) a branch of the infraorbital canal runs dorsad in the antorbital bone (figs. 10 and 11). This is the branch interpreted by JARVIK as the "posterior transverse commissure" (cf. p. 415 in this paper). The same dorsally directed canal branch where it, however runs behind the posterior nostril, is found in *Lepidosteus* as well (ALLIS 1904) and also in *Sinamia* (cf. p. 419 in this paper and fig. 15). In *Polypterus* there is no dorsally directed canal, but the second antorbital bone sends a process dorsad, plainly visible in the larval stages (fig. 16). The antorbital dorsal canal branch in *Amia* and the dorsal process in *Polypterus* run between the anterior and the posterior nostrils. In *Sinamia* the conditions as interpreted by the author (p. 420 in this paper), are the same.

The same dorsal branch of the infraorbital canal is also found in *Birgeria*, *Coccocephalus* and *Glaucolepis* (NIELSEN 1942). In *Brachydegma* the conditions seem to be the same as in the Palaeoniscids and the Holosteans mentioned, although nothing is known about the anterior portion of the supraorbital canal.

In *Cornuboniscus* the alleged supraorbital canal may be divided in one ventral or rostral portion, which belongs to the infraorbital canal as a dorsally directed branch, and one longer, dorsal portion, which runs between the two nostrils as a true nasal portion of the supraorbital canal. The difference is only that whereas in the other fishes mentioned the infraorbital branch runs posterior to the nasal (supraorbital) canal, it runs seemingly as a continuation of this canal in *Cornuboniscus*. If there is an actual junction or anastomosis between the two canals or not has no importance. Probably there is a connection between them in *Cornuboniscus*. In *Borcosomus* the appearance is decidedly in favour of a junction. This connection then corresponds to the junction between the nasal sensory canal and the infraorbital canal in *Lepidosteus* (cf. NIELSEN 1942, p. 206).

The so-called supraorbital canal in the other Palaeonisciform fishes may be interpreted in the same way. Apparently it runs—represented in the figures by dotted lines—down the snout to join the infraorbital canal in the rostral

commissure, but, in reality the canal may be supposed, as in *Cornuboniscus*, to consist of a ventral, infraorbital portion and a dorsal supraorbital.

In this way there is no difference in principle in the pattern of the canal system in the snout in the Actinopterygian fishes (including the Brachypterygians). The circumstance that the nasal canal portion in many Palaeoniscids runs laterally to the nostril is due to the fact that that in these forms only the anterior nostril is developed (or described, so far).

In Palaeonisciform fishes either both nostrils are developed, as is the case in the Carboniferous *Cornuboniscus*, the Permian *Pygopterus* (ALDINGER 1937, p. 144) and the Triassic *Birgeria, Glaucolepis* and *Boreosomus*; or, only the anterior nostril as in the Carboniferous *Canobius, Cycloptygius* and *Nematoptychius* and the Permian *Palaeoniscus*; or, only the posterior nostril as seems to be the case in the Carboniferous *Coccocephalus* and the Triassic *Pteronisculus*. Our knowledge of the snout in Palaeoniscids is, however, so uncertain and spurious that further discoveries will show if the presence of two nostrils is more common than has been supposed. The two nostrils in the Triassic *Perleidus* (STENSIÖ 1921) are probably both to be interpreted as anterior nostrils judging from their position.

NIELSEN (1942, p. 206—207) has to a certain degree tried to interpret the canals in the snout of Palaeonisciform and Holostean fishes in the way indicated above, but not taken the full consequences of his suggestions.

From what is mentioned above, it appears that there may, actually, be a commissure between the supraorbital and the infraorbital canal in Palaeoniscids, but, this commissure does not correspond to either of the two commissures in JARVIK's sense. The dorsal portion of the commissure will correspond to the dorsal portion of JARVIK's anterior commissure and the ventral portion to the ventral portion of JARVIK's posterior commissure.

DEVELOPMENT OF DERMAL BONES.

The stages of *Polypterus* available for this investigation are unfortunately too old to allow any observations concerning the early ontogeny of the dermal bones. Very little is, therefore, to be said concerning the formation of the blastemas. Most of the bones are already formed in the youngest stage at my disposal. The exceptions are practically only the extrascapulars and the suprascapular. The first nasal (os terminale) is already formed as a tiny rod of bone, and the ventral portion of the preopercular which forms separately is also present as a bone scale of irregular shape.

As to the extrascapulars, the supratemporal cross-commissure in the series of transverse sections is sectioned longitudinally to the course of the canal, a

VOL. 28 1947

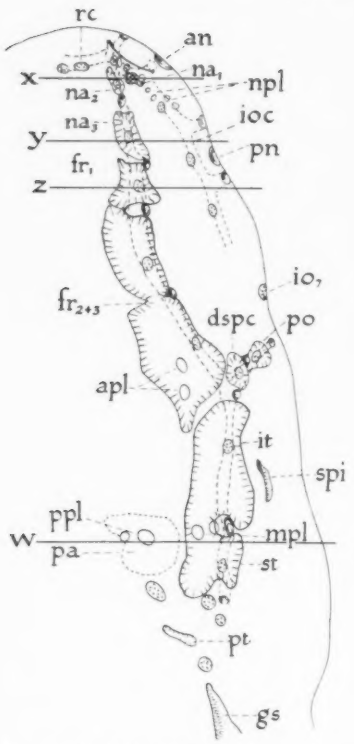

Fig. 17. *Polypterus senegalus*, 24 mm. Cranial dermal bones and sensory organs in dorsal view (24×1). Open circles, pit line organs, dotted circles, neuromasts. x. level of fig. 18. y. level of fig. 19. z. level of fig. 20. w. level of fig. 24.

circumstance that makes reliable observations concerning the development of possible binary blastemas very difficult. The only point where it has been possible to make comparatively trustworthy observations is, therefore, the development of the suprascapular. The result will be recorded in page 442.

Generally speaking it seems that the bones are formed in a slightly different way than is the case in, for instance, *Amia* and even *Lepidosteus* (PEHRSON 1922, 1940, HAMMARBERG 1936). At least it has not been possible to discover any binary bone primordia, not even as far as the first nasal and the extrascapulars are concerned. The bone primordia in the infraorbital line as well as their blastemas, do not develop as binary structures in any fish, as far as is known. As a rule the canal bones in *Polypterus* very soon assume cylinder shape although the walls for some time remain uncompleted, being only imperfectly ossified with irregular perforations. The change from a cylinder to flat bones takes place, in the same way as in *Amia*, by means of lamellae or wing-like processes developing from the tube-like bone (figs. 19 and 20).

Another typical feature in *Polypterus*, as far as can be judged without exception, is that a separate bone primordium develops in connection with each neuromast.

Nasal. According to the terminology used by HOLMGREN—STENSIÖ (1936) there are three nasals in *Polypterus*, as stated by ALLIS (1900). The three nasal elements (viz. the "os terminale", the "accessory nasal" and the "nasal" in TRAQUAIR's description) are the homologues of the nasal in *Amia* which is formed by three primordia.

In the 24 mm specimen of *Polypterus* the first nasal is just beginning to form. In the adult fish it is turned laterad and slightly caudad, and forms a tube round the corresponding portion of the sensory canal. In this young specimen this portion of the canal is not yet formed (figs. 17 and 18). There is a pore opening into the ethmoidal cross-commissure on each side of the snout. Immediately caudally to this pore there is a shallow groove instead of

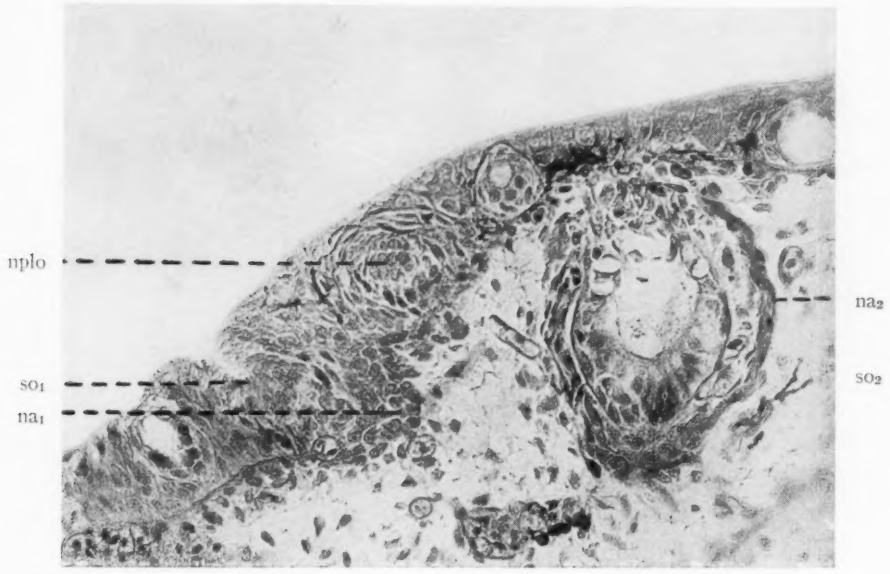

Fig. 18. *Polypterus senegalus*, 24 mm. Cross-section at the level x in fig. 17, showing supraorbital neuromasts No. 1 and No. 2, primordium of nasal bone No. 1, nasal bone No. 2 and a nasal pit line organ. Michrophotogr.

a canal running laterad and somewhat caudad in the same position later held by the sensory canal. A deeper indentation in the rostral end indicates the pore between the portions of the canal enclosed in the first and the second nasal bone.

The groove itself has more the shape of a shallow and narrow fissure formed by a fold of the epidermis slightly overlapping from behind (fig. 18). The neuromast is situated under this fold. Below the sense organ a comparatively thick blastema is formed. In this blastema the primordium of the nasal is beginning to form in shape of a straight, narrow rod (fig. 18). No sign of a binary origin is to be seen either in the blastema or in the bone rudiment.

In a 27 mm specimen, thus, only slightly longer than the youngest specimen, though the nearest in age, development has advanced considerably. It may be mentioned that while there is no sign of the typical, long nasal tubes in the 24 mm specimen, these are formed already in the 27 mm specimen. Nor is an intermediate stage to be found in the development of the nasal bone. The first nasal has already assumed its definite shape and surrounds a well developed canal with the neuromast No. 1, only the distal end of the bone tube is not quite formed. As will be seen from the description, the development in the nasal as well as in the frontal regions of the supraorbital canal progresses rostrad from the caudal end. The bone tube itself is not yet quite ossified. As in all young, tube-like bones in Polypterus, the walls have more or less the

VOL. 28 1947

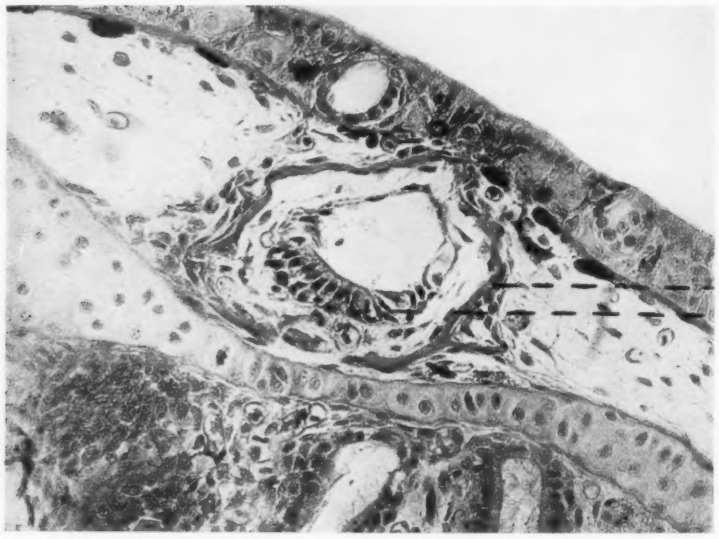

Fig. 19. *Polypterus senegalus*, 24 mm. Cross-section at the level y in fig. 17, showing supraorbital neuromast No. 3 and cross-section of nasal bone No. 3 with beginning formation of flanges. Microphotogr.

shape of a net work of irregular perforations. This is still the case in slightly older specimens measuring up to 45 mm in length. In a 101 mm specimen an unbroken solid wall of bone is formed round the canal.

The second ("accessory") nasal is formed in the 24 mm specimen in shape of a tube-like bone, the walls of which have still the typical irregular perforations (fig. 18). No flanges are formed so far. Not until the 101 mm specimen has the bone assumed its definite shape by developing a medial flange which slightly overlaps the edges of the adjacent medial bone, the rostral. The bone lodges the neuromast No. 2.

The third nasal in the 24 mm specimen has also the shape of a tube but the walls are, though still perforated to a certain degree, more solid than those of the second nasal (fig. 19). The beginning of the formation of flanges is to be seen. In the 37 mm specimen a comparatively broad medial flange is formed and in the 45 mm specimen the medial flange has assumed its definite extension medially, the edges of the right and the left lamella only leaving a narrow space between them, later to be filled up by the caudal process of the rostral.

As already pointed out above, the homology between the three nasals in *Polypterus*, and the single nasal in *Amia*, is firmly established. Further there is no doubt concerning the homology between the nasal in *Lepidosteus* (HAMMARBERG 1937) and the nasal in *Amia*, resp. *Polypterus*. As mentioned by HAMMARBERG the anterior end of the supraorbital canal in *Polypterus* has very much the same shape as the corresponding portion of the supraorbital

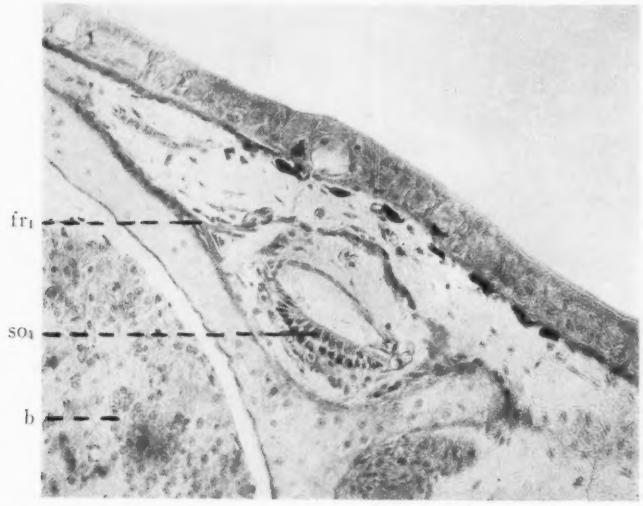

Fig. 20. *Polypterus senegalus*, 24 mm. Cross-section at the level z in fig. 17, showing supraorbital neuromast No. 4 and anterior end of frontal bone with well developed flanges. Microphotogr.

canal in *Lepidosteus*. The difference is only that the nasal canal in this fish not only turns laterad, but, also continues along the lateral edge of the nasal, and ends in the postero- lateral corner of this bone. The anterior portion of the nasal supraorbital canal in *Amia* also makes a lateral bend, more pronounced in larval stages (figs. 10 and 15). The same conditions are also found in *Sinamia* (STENSIÖ 1935), where the nasal canal as in *Lepidosteus* follows the edge of the nasal laterad and caudad (fig. 15). This lateral bend seems to be a characteristic feature of Holosteans and *Polypterus* only. It is lacking in Crossopterygians where the supraorbital canal runs straight rostrad and opens in the ethmoidal cross commissure (at least in *Eusthenopteron*) after a more or less pronounced S-curve, and in Palaeonisciformes, Chondrosteans and Teleosteans.

According to JARVIK (1942), the first nasal (terminal) in *Polypterus* is the homologue of the anterior "tectal" in Coelacanthids. The "tectals", writes JARVIK, are "a longitudinal series of bones in the anterior prolongation of the series of supraorbitals" (JARVIK, l.c., p. 351) and usually called antorbitals in Crossopterygians. They are situated laterally to the nasal series and "primarily not pierced by any sensory canals" (l.c., p. 249). JARVIK considers the "postero-dorsal facial portion" of the premaxillary in *Polypterus* to be a posterior "tectal" (cf. p. 431 in this paper).

JARVIK extends the alleged similarity between *Polypterus* and Coelacanthids to *Sinamia* and *Amia* as well. In the latter fish the anterior "tectal" element is supposed to be the antero-lateral part of the nasal whereas the part of the

antorbital which lodges the infraorbital neuromast No. 5 is said to correspond to a middle "tectal", and the dermectethmoid to a posterior.

As already mentioned (p. 413) JARVIK's interpretations of the homologies of the bones in the snout of Holosteans and *Polypterus* are based on his theories concerning the sensory canal pattern in this part of the head. These theories have already been dealt with in pp. 415—420, and, as they are rejected by the present author there is no reason to enter into any argumentation on the consequences of the theories.

Frontal. This bone is comparatively well developed in the 24 mm specimen, and forms a bone tube round the sensory canal (figs. 16 and 17). The walls of this bone tube, however, are still imperfect and form a sort of network of irregular perforations as was also the case in the nasal. Medially a horizontal lamella is formed which broadens caudad. The caudal portion of the bone is thicker and generally better developed than the rostral end. Laterally there is a narrow lamella developed (fig. 20).

The frontal is formed in connection with the supraorbital sense organs Nos. 4, 5 and 6 (the terminal organ counted as No. 1), a pore being formed between each neuromast. On a level with the first pore on each side there is a suture in the bone (fig. 17). A separate first frontal is thus formed in connection with the supraorbital sense organ No. 4. Where the second frontal pore lies there is no suture to be seen, but, there is a deep incision in the lamella. This seems to indicate that also this part is formed from two separate primordia. The frontal is, thus, ontogenetically, according to all appearances, formed from three separate primordia, one in connection with each neuromast. The state of development tells further that the formation has begun with the caudal end and progressed rostrad, like the three nasal bones. There is no indication of a binary origin of either of the three frontal elements, a circumstance that hardly could be expected considering the rather far advanced development of the bone.

While in the 24 mm specimen the third nasal is still a perforated bone tube with a narrow lateral lamella the frontal, even the anterior element, is far more advanced and has formed a broad flange laterad as well as mediad.

In *Amia* (PEHRSON 1940) the frontal lodges the supraorbital neuromasts Nos. 4—6 as in *Polypterus* but there the primordia are formed in connection with the neuromasts 5 and 6 and are distinctly binary. These primordia fuse transversally and then lengthwise. In connection with sense organ No. 4 no separate primordium is developed in Amia, but the rostral end of the fused original primordia grows rostrad till it reaches and eventually incorporates even this neuromast. In *Amia* there is first a gutter-like bone formed which closes to form the bone tube. It is not possible to decide if the bone is formed in the same way in *Polypterus,* as sufficiently early stages are missing.

Nevertheless the conditions in *Polypterus,* where one bone is formed in connection with each separate neuromast in the supraorbital line, has to be considered as more primitive than in Amia.

Rostral. This bone is formed in the 24 mm specimen and has the shape of a bone cylinder round the rostral cross canal. The walls have the irregular perforations typical of the young canal bones in *Polypterus.* It is not possible to discover any signs of the bone having originated from a left and a right hand primordium, nor of the primordium having been binary. A short dorsal lamelliform process is already formed (fig. 16).

During the subsequent stages, the bone tube consolidates in the usual way and the dorsal lamelliform process grows in length and thickness till it has reached the normal extension in relation to adjacent bones in the 101 mm specimen.

The canal lodges organ No. 1 in the infraorbital canal on each side and thus corresponds to the median portion of the rostral in Amia where there are altogether four neuromasts associated with the rostral.

OL.
28
947

"*Premaxillary.*" The neuromast No. 2 in the infraorbital canal is situated in the portion of the canal which makes a sharp bend ventro-laterad (fig. 8). This portion of the canal is surrounded by a short tube-like bone entirely free from the premaxillary which is already formed and lies close mediad to the canal bone (fig. 16). The latter might be considered as the homologue of the lateral part of the rostral in *Amia.* In this fish the rostral lodges four neuromasts of which the two middle ones correspond to the two neuromasts in the rostral of *Polypterus.* If this surmise is correct, the bone lodging the infraorbital organ No. 2 in *Polypterus* should be named a *lateral rostral.*

At the ventral end of this ventro-laterally directed portion the canal turns caudad and then runs practically straight in this direction. In the anterior portion of this canal section the neuromast No. 3 is situated. This portion is also surrounded by a canal bone, but the bone does not form a cylinder round the canal. Medially, towards the lateral margin of the planum nasale the canal bone is open and the wall is formed by the premaxillary (sensu strictu). Thus, the roof, the lateral wall and the lateral part of the roof are covered by the canal bone which has the shape of a gutter instead of a tube. Judging from its position it is to be considered as an antorbital, and as there is another bone to follow, this one will be termed the first *antorbital.*

In this young stage the canal bone, like the ones described previously, is perforated irregularly. It is doubtful if it is entirely free from the premaxillary. It is not possible to decide with certainty if the perforated lamellas of the growing premaxillary are fused or not in some places with the irregularly shaped edges of the antorbital.

Yet from the fact that the first infraorbital is entirely free from the premaxillary, it seems permissible to conclude that this has been the case in a

slightly younger specimen. And it may possibly be so even in this specimen. In the next oldest specimen measuring 27 mm, however, the first antorbital as well as the lateral rostral are fused with the premaxillary.

The next bone in caudal direction lodges neuromast No. 4 (fig. 16). It forms a complete cylinder round the canal. It is further developed than the anterior bones and seems to have been formed earlier. It should be termed the *second antorbital*, judging from its position. The medial side carries a slightly protruding ridge, which runs along almost the whole length of the tube-like part of the bone. The posterior end of this ridge is prolonged into a dorsally directed lamella which lies in the shape of a thin blade close to the nasal capsule. Anteriorly the ridge has a couple of small branching connections with the premaxillary.

The two antorbitals together correspond to the antorbital in *Amia*, but, whereas the antorbital in *Amia* lodges four neuromasts there is only one in each one of the two antorbitals in *Polypterus*. Furthermore the antorbital in *Amia* is formed as one single primordium notwithstanding the large number of neuromasts. But there is one resemblance between the two antorbitals in *Polypterus* and the single bone in *Amia*. In both fishes there is a pronounced dorsal process. In *Amia*, as in *Sinamia* and *Lepidosteus* this process is formed by the canal and lodges (at least in *Amia* and *Lepidosteus*) a neuromast but in *Polypterus* it has the shape of a lamelliform outgrowth. If this process should be judged as the homologue of the dorsal portion of the antorbital of *Amia* it might be considered as a suppressed part of the canal bone. Embryological evidence for this suggestion is lacking so far, no sufficiently young stages of *Polypterus* being at hand.

In older stages the connection between the second antorbital and the premaxillary becomes more definitely developed.

The *premaxillary* (sensu strictu) is a comparatively broad plate (figs. 16 and 28). Anteriorly it has a narrow projection lateral to the short chondral rostrum. To the greater part it is situated underneath the lateral parts of the planum nasale. The anterior portion of the plate is slightly bent dorsad as is the premaxillary in *Amia*. On a level with the anterior end of the second antorbital it narrows considerably and is fused with some strands of bone tissue to this bone. The lateral margin of the bone carries the teeth.

Like the "maxillary" which will be dealt with below, the "premaxillary" in *Polypterus* has also been the subject of interpretations in various directions. According to ALLIS (1900), the tooth-bearing bones forming the upper jaw in *Polypterus* correspond in *Amia* to the premaxillary bone without its posterior process, the antorbital and the lateral part of the ethmoid (rostral). HOLMGREN —STENSIÖ (1936) consider it to be built up by one premaxillary component and one sensory canal component and term the bone accordingly the premaxillary-antorbital. Another opinion is launched by WESTOLL (1936). He

refers to MOY-THOMAS (1934) who had emphasised that the teeth of bony fish were formed separately from the bones which afterwards bear them. Teeth might also be "attached to a lateral-line bone developed in the near neighbourhood without the formation of separate tooth-bearing rudiments". WESTOLL concludes that the toothbearing lateral line bones in *Polypterus* for instance "can easily be interpreted in this way without any compound names for which there is no embryological evidence".

The results of the study of the skull of the 24 mm *Polypterus* verify the opinion maintained by HOLMGREN—STENSIÖ and even by ALLIS: the "premaxillary" is a complex bone formed by a tooth-bearing premaxillary component, homologous to the premaxillary in *Amia,* and three separate canal bone components, homologous to the lateral part of the rostral and the entire antorbital bone in *Amia.*

There is no instance amongst recent fishes known to the author where the premaxillary is fused with canal bones. Yet in fossil groups, viz. Crossopterygians and Palaeoniscids the "premaxillary" is often a complex bone. Unfortunately the rostral end of the skull is comparatively little known, at least as far as the dermal bones and the course of the sensory canals are concerned, chiefly owing to the imperfect state of preservation of this part in a fossil fish. Judging from the information given by the palaeontological literature, especially the illustrations, there seems to be a complex rostro-premaxillary at least in *Osteolepis, Eusthenopteron, Laugia* and *Macropoma* amongst the Crossopterygians, perhaps even in *Megalichtys* and *Rhabdoderma.* This bone is termed the "dentigerous rostral" by WESTOLL (1936), but consists of a rostral fused to the premaxillary. In *Polypterus* the median rostral is a typical canal bone without teeth whereas the lateral rostral and the antorbitals are fused with the premaxillary.

Similar conditions exist in most of the palaeozoic Palaeoniscids as far as studies of the literature will disclose, and even in Triassic forms (*Oxygnathus* and *Boreosomus* for instance). Amongst the forms where the structure of the dermal skeleton of the snout is known, only *Cheirolepis* is an exception, as WATSON's reconstruction shows a free rostral bone (WATSON 1925). Yet WESTOLL (1937) has expressed some doubts as to the correctness of WATSON's interpretation of this fish. It seems probable that also the structure of the snout in *Cheirolepis* might follow the same scheme as the rest of the primitive Palaeoniscids. It seems that in the primitive forms at least the premaxillary should be fused with rostral elements as well as with the antorbital. In *Birgeria* (STENSIÖ 1932), with reservation because of the imperfect condition of the snout, there may possibly be a free antorbital with the typical dorsal branch of the canal and the premaxillary should be fused only with antorbital elements.

Lacrimal. In the 24 mm specimen this bone is developed as a typical canal bone and lodges the fifth infraorbital neuromast (fig. 16). It is entirely free

from the "maxillary" and so is still the case in the 101 mm specimen. According to HOLMGREN—STENSIÖ it is fused in the caudal end to the "maxillary" in a 30 mm specimen of *Polypterus lapradei*. In *Polypterus senegalus*, anyhow, the bone seems to remain an independent element in the infraorbital row of bones.

In *Amia* the lacrimal lodges the neuromasts Nos. 7 and 8, but develops from one single blastema.

Infra-(sub-)orbitals. In *Polypterus* there are two infraorbitals (fig. 16). The first of them lodges the sixth infraorbital sense organ. In the 24 mm specimen it has the shape of a bone cylinder like the lacrimal. However, it is situated quite near to the maxillary, and aggregations of cells between the lamelliform branching processes of the maxillary indicate the beginning fusion with this bone. It is still an independent bone in the 24 mm specimen.

Caudally to the infraorbital No. 1 the canal is not yet formed and has still the shape of a shallow gutter, at the bottom of which the neuromast No. 7 is situated. Nevertheless a bone is already formed but as no canal is formed it has the shape of a rounded disk bent to the shape of a gutter (fig. 16). Caudally to the sense organ this bone is separated from the maxillary only by means of a stratum of cells.

Already in the next stage, the 27 mm specimen, the infraorbital I is fused with the maxillary in its whole length. Also the infraorbital II is fused to the maxillary, although so far only partially.

In the 24 mm specimen the so-called maxillary of the adult still consists of several distinct parts, two free infraorbital canal bones and the maxillary sensu strictu. This latter element of the future complex bone consists of an anterior portion which bears teeth and of a posterior toothless portion. The anterior portion has the shape of a comparatively broad, triangular, flat bone. One side of the triangle is directed rostrad (fig. 28). The medial margin of this triangular part is to a great extent covered from below by the dermo-palatine. Teeth are placed along the lateral edge of the triangle. The most caudal teeth are situated under the anterior half of the eye. The toothless part of the maxillary stretches caudad under the posterior half of the eye and beyond the eye in a caudal direction. This posterior half of the bone has a different shape from the tooth-bearing part (fig. 16). While the anterior end is a comparatively broad, horizontal plate, the bone tapers caudad into an almost cylindrical rod, on the medio-ventral side of which the most caudal teeth are situated. These teeth protrude chiefly in a medio-ventral direction and are not visible in profile, in this stage at least. Behind the most posterior teeth the maxillary acquires the shape of an almost perpendicular lamella situated in the maxillary fold. The dorsal edge of this lamella is thicker than the rest and bent mediad, thus forming a sort of mediad open gutter. The rostral prolongation of the preopercular fits in this gutter. This preopercular prolongation reaches rostrad under the posterior third of the eye. Here the maxillary bends dorsad and tapers

VOL 28 194

gradually into a fine needle-like structure which, however, continues rather far in a dorso-caudal direction.

The "maxillary" in *Polypterus* is thus like the premaxillary a compound bone. The tooth-bearing part is developed as a normal maxillary in fish in principle. Only the long caudal prolongation is a distinctive peculiarity, unparalleled in recent fishes. The morphological significance of this formation will be dealt with below. In addition to the maxillary proper the complex bone is formed by two canal components which correspond to the two suborbitals in *Amia*. The "maxillary" should thus be termed a maxillary-infraorbital.

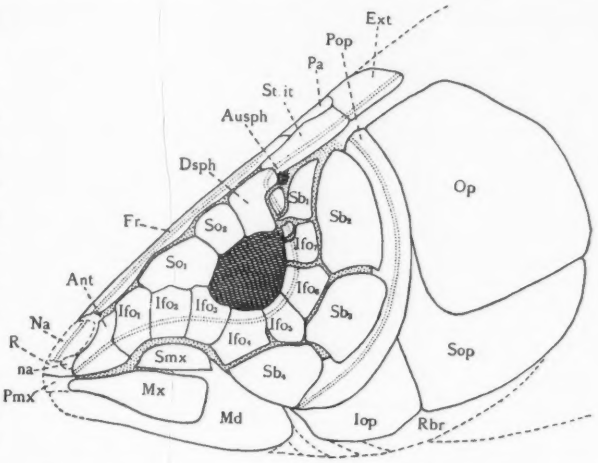

Fig. 21. *Lepidotus semiserratus*. Skull in lateral view (from HOLMGREN—STENSIÖ). *Ant* antorbital; *Ausph* autosphenotic; *Dsph* dermosphenotic; *Ext* extrascapular; *Fr* frontal; *Ifo*$_1$—*Ifo*$_7$ infraorbital bones; *Iop* interopercular; *Md* mandible; *Mx* maxillary; *Na* nasal (-postrostral); *Op* opercular; *Pa* parietal; *Pmx* premaxillary; *Pop* preopercular; *R* rostral; *St.it* supratemporo-intertemporal; *na* nostril.

NIELSEN has described a similar complex maxillary in *Glaucolepis* (fig. 27), called maxillo-infraorbital (1936) or lacrimo-maxillary (1942).

The development of the "maxillary" in *Polypterus* reminds one in a striking way not only of the "premaxillary" in this fish but also of the "dentary" in Actinopterygians. These three bones are complex bones, built up of a component formed independently from the sensory canal. This is in sensu strictu the maxillary, the premaxillary and the dentary, all three tooth-bearing bones. These bones fuse later with sensory canal components, in the case of the premaxillary and the maxillary from the infraorbital line, and in the case of the dentary from the mandibular line (PEHRSON 1940 and 1944, cf. 443 p. in this paper).

Not even in the 24 mm specimen is there any indication of an independent origin of the posterior process of the maxillary. Yet, the thought cannot be entirely dismissed that this portion of the bone might be the homologue of a *supramaxillary*. A supramaxillary is found in *Aspidorhynchiformes* and in *Amiiformes* as *Lepidotus* (fig. 21), *Sinamia* and *Amia*. In *Amia* it develops comparatively late (PEHRSON 1940) in the caudal part of the maxillary fold. In *Polypterus* the anterior portion of the maxillary is situated in a fold, the homology of which with the maxillary fold is at least disputable (ALLIS 1900).

On the other hand the portion of the posterior half of the maxillary, which is situated under the eye, is enclosed in a fold or lip which lies posterior to the fold where the labial cartilage is enclosed. The position of this part of the maxillary, at least, corresponds more to the position of the supramaxillary in *Amia*.

Also the so-called maxillary in *Polypterus* has been the subject of varied interpretations. ALLIS (1900) suggests that the so-called maxillary bones in *Polypterus* probably are the homologues of the dermopalatines in *Amia* and Teleosts. HOLMGREN—STENSIÖ on the other hand consider this bone to be a complex bone like the premaxillary. The anterior component should be tooth-bearing and correspond to a real maxillary. Caudad it should continue to join ventrally the second component, a canal bone. The canal bone should be fused to the maxillary component in a narrow isthmus only. As the last teeth of the tooth-bearing portion of the bone belong to the canal bone component, the authors suggest a prolongation still more caudad of the maxillary portion.

Before the discussion of the morphological significance of the maxillary in *Polypterus*, attention has to be drawn to the so-called *quadrato-jugal*. From the point where the maxillary in the 24 mm specimen turns dorsad and leaves the maxillary fold, it is continued caudoventrad by a thin membrane (fig. 16). This membrane is well delimitated from the surrounding connective tissue but is, because of its thinness, difficult to describe as bone. It is separated from the maxillary by a very narrow fissure. The caudal portion of the lamella which lies outside the anterior portion of the musculus adductor mandibulae gets thinner caudad and changes imperceptibly into connective tissue.

The membrane remains in the same state during the nearest following stages but in the 101 mm specimen it has changed into a real bone. This bone, in older specimens represented by two (HOLMGREN—STENSIÖ), is the bone termed "y" by TRAQUAIR. The bone in the 101 mm specimen corresponds to the anterior of the two bones represented in fig. 298 in HOLMGREN—STENSIÖ. Caudally to the bone the presence of a thick and well marked sheet of connective tissue indicates the later formation of the posterior of the two bones. In HOLMGREN—STENSIÖ both bones are called quadrato-jugal (although with a question mark) and considered as related to the sensory canal bones because of the alleged presence in this part of a line of pits (the primary mandible pit line [HOLMGREN 1942]; the quadrato-jugal pit line [JARVIK 1947]). As pointed out by JARVIK (l.c.) this line, however, is situated in the skin over the posterior of the two bones in question and probably has nothing to do with the development of the anterior of the two bones. According to JARVIK, this bone represents a posterior independent part of the maxillary. It is possible that this is the case, as will be developed below.

JARVIK (1947, p. 67) suggests that the anterior bone corresponds to the posterior part of the maxillary in Osteolepiform Crossopterygians, but declares

that the maxillary in *Polypterus* is much reduced as is the case in the Coelacanthids. Now one result of the investigation that has led to this paper is that the maxillary in *Polypterus* far from being an insignificant part of a complex bone, is on the contrary, a very substantial portion of the bone in question. The maxillary is missing as a rule in the Coelacanthids described so far. Only in *Wimania* STENSIÖ (1921) has found a bone which is termed maxillary in the representation of the head but which is called only a "supposed maxillary" in the text. The maxillary in the Coelacanthids was probably only represented as in *Latimeria* by small tooth-bearing plates.

In the larval *Polypterus,* the maxillary is on the contrary a well developed bone forming not only a typical, large horizontal, tooth-bearing portion but also an elongated caudal process, possibly the homologue of a supramaxillary (p. 435). In the adult it broadens considerably and forms (with the fused infraorbitals) not only the ventral delimitation of the orbit but also a part of the covering of the cheek. Besides, it continues still further caudad under the large cheek-plate formed by the preopercular (ALLIS 1922). This part of the problem will be dealt with further in connection with the ontogeny of the preopercular (p. 445).

If comparisons with fossil fishes are to be drawn there is another group to which attention should be paid, the *Palaeonisciformes.* As is known, all the palaeozoic and little specialised members of this group possess a well developed maxillary, the anterior portion of which has the shape of a horizontal plate. Posterior to the eye the maxillary continues as a vertical, broad lamella which stretches very far caudad. Often even the caudal end of the maxillary has a postero-ventrally directed portion, as in the families belonging to the suborder *Palaeoniscoidei* (BERG 1940). There are strong teeth along the whole margin of both the horizontal and the vertical portion (fig 27).

The Osteolepid maxillary is not so strongly developed. This concerns the anterior, horizontal portion as well as the posterior vertical. The vertical portion gets narrower at its posterior end, where the quadrato-jugal is interposed between the maxillary and the preopercular. In the *Palaeonisciformes* the maxillary continues without getting narrower till it reaches the preopercular.

It may be suggested that the so-called anterior quadrato-jugal in *Polypterus* corresponds to the caudo-ventral end of the maxillary in the *Palaeonisciformes.* This part may have acquired independence perhaps in connection with the loss of the caudal row of teeth.

As to the second so-called quadrato-jugal in *Polypterus,* it is formed near the quadrato-jugal (or primary mandibular) pit-line. The bone develops ontogenetically in a sheet of connective tissue as does the anterior of the two bones. In a 101 mm specimen where this second bone is still missing there is in the place of the future bone the same formation of connective tissue as there

is in young specimens of *Polypterus* where the anterior bone is going to develop.

An independent quadrato-jugal exists in Crossopterygians but has long been considered missing in Palaeonisciform fishes. Yet, already WATSON (1925) suggested the possibility of the existence in *Cheirolepis* of a quadrato-jugal. Later NIELSEN (1936) has shown that there is a quadrato-jugal bone anterior to the anterior edge of the lower part of the preopercular in *Glaucolepis*. It is partly covered by the maxillary and only a small part shows from the outside of the cheek (fig. 27). As the anterior part which is overlapped by the maxillary only consists of a thin lamella, NIELSEN is inclined to believe in an incipient reduction of the bone, due to the backward growth of the maxillary. NIELSEN has found a pit-line on the uncovered part of the bone in some specimens of *Glaucolepis*.

This pit-line is considered by NIELSEN (and other authors) to be the vertical pit-line of the cheek. In *Polypterus* this line is situated on the preopercular and in close connection with the horizontal pit-line of the cheek. It seems likely that the so-called quadrato-jugal pit-line and the vertical pit-line in *Polypterus* are both different portions of the same line, an opinion also suggested by JARVIK (1947) although he includes the "secondary mandibular line" as well. In that case the vertical pit-line in *Palaeonisciformes* is homologuous to the entire vertical pit-line in *Polypterus* or part of it, and the quadrato-jugal in *Glaucolepis* (and other *Palaeonisciformes*) is the homologue of the second "quadrato-jugal" in *Polypterus*.

Postorbital. The single postorbital in *Polypterus* is developed as a cylindrical canal bone in the 24 mm specimen and lodges canal organ No. 8. There is nothing of interest to add concerning the bone at later stages.

Dermosphenotic. In the 24 mm specimen this bone is developed as a normal tube-like canal bone lodging the infraorbital neuromast No. 9. Already in the 27 mm specimen it begins to fuse with a perichondral ossification on the lateral edge of the taenia marginalis, the future "sphenotic". The neuromast is innervated in the usual way by a special nerve, branching off from the root of the facialis.

According to HOLMGREN—STENSIÖ (1936) the dermosphenotic in the adult is inseparably fused to the sphenotic as a superficial covering of this bone.

ALLIS (1922) terms the complex bone the postfronto-sphenotic.

Intertemporo-supratemporal and *parietal.* In the 24 mm specimen the intertemporo-supratemporal is just formed (figs. 16 and 17). The anterior, intertemporal portion consists of a well developed cylindrical bone formed round the canal and lodging a canal organ innervated by the ramus oticus. The bone cylinder is furnished with a comparatively broad medial lamella. The lamella developed on the lateral side of the bone is narrower. On the level of the pore between the intertemporal and the supratemporal portions of the bone the

lateral lamella has a deep incision which divides the bone into a long intertemporal portion and a shorter supratemporal. There is no incision corresponding to the lateral one on the medial lamella. The lateral lamella of the supratemporal portion is not so well developed as that of the intertemporal. The supratemporal part of the bone is in other respects developed like the intertemporal. The bone tube lodges the canal organ innervated by the nervus glossopharyngeus.

The intertemporal and the supratemporal portions on the right side are still separated by a narrow fissure which divides not only the lateral lamella but also the medial lamella as well as the cylindrical part. The conditions on this side prove that the bone is formed in two portions, each one in connection with the corresponding neuromast. This is in agreement with the principle, pointed out before that each separate canal bone in *Polypterus* is formed in connection with the only one single neuromast, or rather that one canal bone is developed in connection with each neuromast.

OL.
28
947

On a level with the pore between the inter- and the supratemporals two pit lines are developed, the middle and the posterior lines of pits of the head. As the figure (17) shows the middle pit line is situated on the median lamella of the bone on the right side and just where the intertemporal and the supratemporal elements meet on the left side. This pit line consists of two sense organs on each side. The posterior pit line has only one sense organ on the left side and two on the right. In connection with the posterior pit line there is a thin bone-like membrane developed on each side (figs. 17 and 24). This a vestigial *parietal* primordium. Rostrad it does not reach much further than the supratemporal and caudad it stretches as far back as the future supratemporal canal commissure which is still undeveloped and marked only by one sense organ on each side. The two primordia do not get in contact with the supratemporo-intertemporals nor do they meet on the mid line.

In the 27 mm specimen which, as has been pointed out before, is considerably more advanced than the slight difference in length might indicate the two components of the intertemporo-supratemporal have fused to one single bone plate where nothing indicates the double origin. The lateral and medial lamellas are still more developed, especially the medial supratemporal lamella, which has grown so far mediad that it has even pushed its edge partly under the posterior pit line (figs. 22 and 25). A remarkable fact is that the insignificant primordium of the parietal, already developed in the 24 mm specimen, still exists but has not grown. While the intertemporo-supratemporal has grown considerably, partly because of its own rapid development, partly in connection with the general growth of the fish, the parietal primordium has kept the same size (as shown by measurement, cf. figs. 17 and 22) and position. It is apparently situated nearer the midline than in the next older stage because of the general growth of the head. Between the medial margin of the supratemporal and the

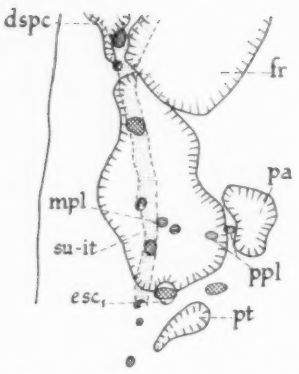

Fig. 22. *Polypterus senegalus*, 27 mm. Supratemporo-intertemporal and parietal primordium in dorsal view (24×1). Circles with crossed lines, neuromasts, circles with horizontal lines, pit line organs.

parietal there is a dense aggregation of cells which establish the growth of the supratemporal.

In a 29 mm specimen the margin of the intertemporal, as well as of the supratemporal part have progressed still further mediad (fig. 26), but, there is still a remnant left of the parietal primordium, which is smaller not only relatively but absolutely, than in the previous stage. In the 37 mm specimen (fig. 23) there is not much left of the original fontanella between the intertemporo-supratemporals either. The intertemporal portions leave only a small cleft between them, and the supratemporal portions almost meet on the mid line.

From the description given above it is clear that a rudimentary parietal develops in the young larva of *Polypterus* but soon disappears. Furthermore it elucidates that separate intertemporals and supratemporals develop. During the ontogeny the separate primordia of the intertemporals and supratemporals on each side fuse to form a complex intertemporo-supratemporal on each side. The fontanella between these two bones is gradually filled up because of the growth mediad of the margins of the bones, and the parietal disappears entirely. The so-called parietal or intertemporo-supratemporal in *Polypterus* is only formed by the two intertemporo-supratemporals, and a parietal sensu strictu does not exist in this fish, not even as a component of a complex bone.

It is not usual for that a dermal bone to develop from a pit line organ, but in *Acipenser* (PEHRSON 1944) the parietal is formed in the same way as in Polypterus only from the middle head pit line. The difference is furthermore that in *Acipenser* a short sensory canal is formed in the parietal. It is possible that has been the case even in the ancestors of *Polypterus*. The canal is, however, suppressed and the parietal degenerates and its position is taken by the intertemporo-supratemporal.

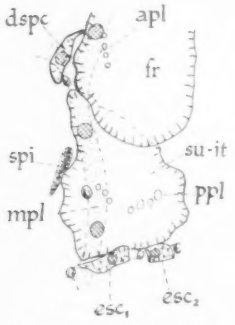

Fig. 23. *Polypterus senegalus*, 37 mm. Supratemporo-intertemporal in dorsal view (15.5×1). Circles with crossed lines, neuromasts, open circles, pit line organs.

From another point of view, the result is that the middle and posterior pit lines of the head, which play an important part for the homologization of the parietal in *Polypterus*, are situated on the intertemporo-supratemporal instead of being supported by the parietal. To a certain degree that is already the case in the 24 mm specimen where at least the middle pit line is placed over the line where the intertemporals and the

VOL 28 194

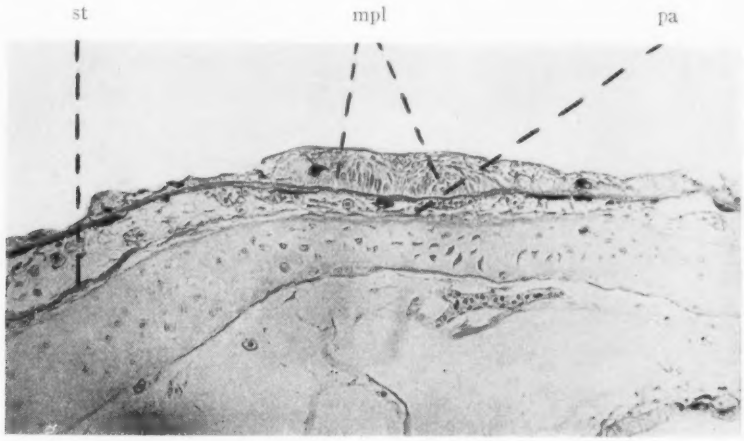

Fig. 24. *Polypterus senegalus,* 24 mm. Cross-section at the level w in fig. 17, showing a middle head pit line sense organ and parietal primordium. Microphotogr.

VOL. 28 1947

supratemporals meet and later fuse. It is possible, however, that in a still younger specimen than the 24 mm at hand, where the intertemporals and the supratemporals are not yet developed, the parietal primordium has stretched still further laterad. Pit lines may then have had the position where a large parietal has developed in the ancestors of *Polypterus.*

From the point of view of homologizing bones in adult forms, where the ontogeny is not known or cannot be known as is the case with fossils, the value of the pit lines as arguments in a discussion on homologies is considerably reduced, however.

This bone is called the parieto-dermopterotic by ALLIS (1922), who considers it to include only the dermal component of the squamosal of the *Teleostei.* Notwithstanding the fact that the dermal component of the "squamosal" in the Teleosts may correspond only to the intertemporal portion of the bone (PEHRSON 1944 a), ALLIS's surmise is quite adequate. On the other hand ALLIS considers in a later work (1935) that the bone he called dermopterotic in *Polypterus* has fused with the parietal to form the bone he called the parieto-dermopterotic.

The bone is supposed to be a complex structure by HOLMGREN—STENSIÖ (1936), formed by the intertemporo-supratemporal and a parietal component, the latter being indicated by the presence of the middle pit line.

Extrascapulars. The development of these bones offers nothing of any particular interest. The two lateral extrascapulars are formed in the 27 mm specimen as a small shield-like bone not much larger than the overlying neuromast (fig. 22). In the 29 mm specimen it has attained cylindrical shape. As to the two medial extrascapulars, there is no indication of them in the 32 mm

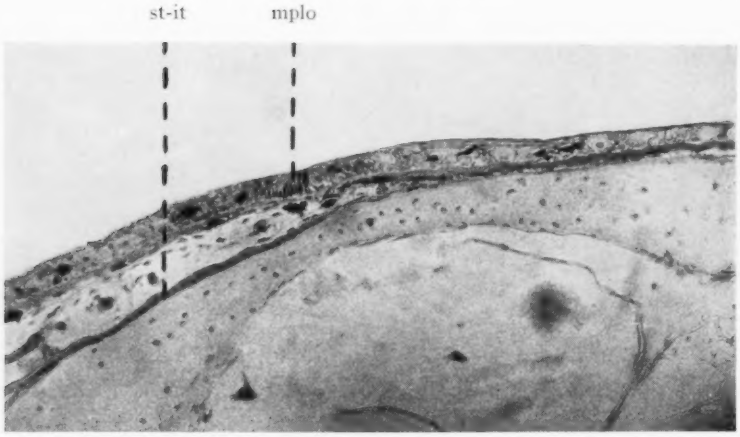

Fig. 25. *Polypterus senegalus,* 27 mm. Cross-section at the same level as in fig. 24. Microphotogr.

specimen. In the 37 mm specimen they are formed in the shape of bone tubes (fig. 23). Each bone lodges one neuromast.

Contrary to ALLIS (1922), the author considers these four bones as the equivalents of the whole of the single extrascapular in *Amia* (PEHRSON 1940). In this fish the supratemporal commissure lodges six neuromasts altogether, three on each side, but Amia has generally a higher number of neuromasts than *Polypterus*. The intertemporal in *Amia,* for instance, has two neuromasts, and this part of the complex intertemporo-supratemporal in *Amia* is formed by two separate primordia to which becomes added one supratemporal primordium which lodges only one neuromast. In *Polypterus* there is only one neuromast in each part of the complex bone, yet, there is no reason to compare the intertemporal primordium in *Polypterus* with only half the intertemporal primordium in Amia.

ALLIS terms the bones in the supratemporal commissure in *Polypterus,* as the single bone in *Amia,* supratemporals and then includes the bone formed round the portion of the main lateral canal situated immediately caudally to the point where the supratemporal canal joins the main canal. This bone is called the *suprascapular* in the terminology used by the present author. The first rudiment of this bone is visible in the 29 mm specimen. No canal is formed so far, but the invagination is just beginning and the future canal has still the shape of a groove. Under this groove the first primordium is formed as a small bone bent to form a shallow gutter.

As far as most canal bones are concerned in *Polypterus,* there has not been an opportunity of studying the first primordia, the blastemas which are the forerunners of bone. The suprascapular is an exception. It is interesting to

VOL
28
194

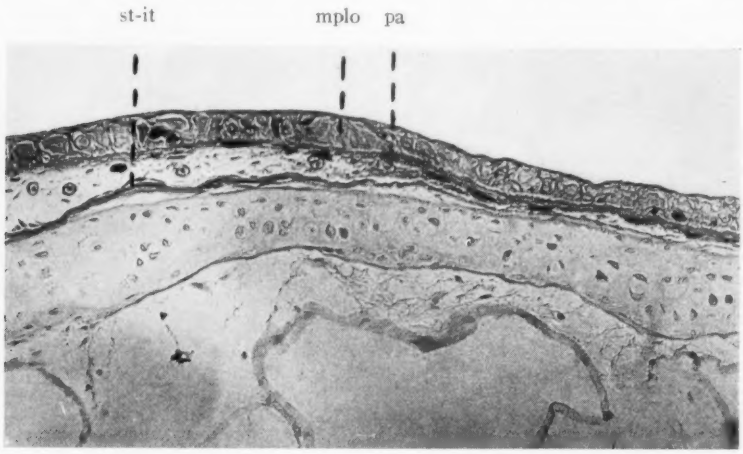

Fig. 26. *Polypterus senegalus*, 29 mm. Cross-section at the same level as in figs. 24 and 25. Microphotogr.

VOL. 28 1947

state that this bone is obviously derived from binary primordia, as is the case with all canal bones in Amia except the bones in the infraorbital line.

In a 32 mm specimen the invagination of the sensory canal is completed but the bone is still gutter-like. In the next stage available, a 37 mm specimen, even the bone has formed a cylinder.

Posterior to the extrascapulars is another bone which forms comparatively early as it already exists in the 24 mm specimen (fig. 17). ALLIS calls it the *posttemporal*. It is formed without any connection with the sensory canal. It does not correspond, at least judging from the ontogeny, to the canal bone formed in connection with the neuromasts in the canal posterior to the supra-scapular in *Amia* or other Ganoids, the *supracleithral*. On the other hand the position corresponds to the place of that bones. As in *Polyodon* (PEHRSON 1944) where it is a canal bone, but has a large vertical lamella, this bone as well consists of a narrow horizontal portion and a comparatively big vertical lamella.

The mandible in the adult *Polypterus* consists of five dermal elements of which two, the dentary and the angular, are complex bones.

The *dentary-splenial* in the 24 mm specimen is already a well developed tooth-bearing bone which covers a little more than the anterior half of the Meckelian cartilage on the outside (fig. 16). The anterior end of the mandibular sensory canal with the first neuromast is situated on the ventral side of the mandible. The canal runs along the whole length of the mandible except the most anterior end. It lodges altogether 5 neuromasts. The anterior end of the canal with the first neuromast is surrounded by a typical cylindrical canal bone. This bone,

the splenial bone No. 1, is at this stage entirely free from the dentary. The portion of the mandibular sensory canal which lodges the neuromasts No. 2 and 3 is also surrounded by bone, but the splenials are here fused to the dentary, except in the anterior end of the canal belonging to neuromast No. 2, where the canal bone is free from the dentary. The complex dentary is thus built according to the same principles described concerning the maxillary and the premaxillary. The development of the canal bones has started at the posterior end of the series and progressed rostrad. The splenials No. 2 and 3, which according to all probability have formed as independent canal bones like No. 1, have already fused with the dentary to form the complex dental-splenial. Already in the 29 mm specimen the first splenial as well has fused with the dentary. The bone is thus completed in this specimen and has assumed its definite structure as a complex bone formed by the dental and the splenials Nos. 1, 2 and 3.

The development of the complex dental-splenial has been described by the author in *Amia* (1940) and in *Esox* (1944). In *Lepidosteus* (HAMMARBERG (1937) has described two independent splenials in a 18.3 mm specimen. They are shaped like slender rods of bone and are fused to the dentary already in a 18.7 mm specimen. In *Polypterus* the first splenial, att least, has assumed the shape of a typical canal bone before it loses its independence. It is not possible to discover if that is the case with regard to the two posterior splenials until still younger specimens have been available for examination. In any case, the existence of a free cylindrical splenial is to be considered as a primitive feature in Polypterus. In *Amia* where the splenials take their origin as binary bony scales, the primordia are attached to the dentary from the beginning. The same is the case in *Esox* where the primordia, however, are still more insignificant than in *Amia*.

As mentioned above there is another complex bone in the mandible, the *angular-splenial*. In the 24 mm specimen two splenials lodging the canal organs Nos. 4 and 5 are already attached to the angular component, which has assumed the definite shape in the adult (fig. 16). In Amia the angular splenials, at least the posterior elements form independently. It seems probable that the splenial components in *Polypterus* have developed as independent bones and subsequently fused with the angular.

ALLIS (1932) terms the dental-splenial only dental, and the angularsplenial the dermarticular. HOLMGREN—STENSIÖ (1936) use the terms dental-splenial and angular respectively.

ALLIS has chosen the name splenial for the large dermal bone which covers most of the medial side of the mandible. This bone is the *prearticular* in the terminology of HOLMGREN—STENSIÖ. In the 24 mm specimen the bone is already a large structure tooth-bearing and possessing a well developed "coronoid" process (fig. 16). In the angle between the anterior ends of the dentals

there is a small tooth-bearing bone on each side. This bone corresponds to coronoid No. 1 in *Amia* which has the same position and is tooth-bearing. In Amia a series of not less than four coronoids is developed. In a 37 mm specimen of *Polypterus* a second coronoid is developed immediately behind the first. At this stage there is still a small gap between the second coronoid and the next bone in the row, the so-called prearticular. In a 101 mm specimen this gap is closed because of the enlargement caudad of the second coronoid and rostrad of the "prearticular". The medial side of the mandible is thus covered by a row of three tooth-bearing bones, as is the medial side of the mandible in *Amia*, the only differences being that there are four comparatively small bones of almost equal size in *Amia*, but two small ones and one very large in *Polypterus*. The two rows of bones are obviously homologous, and the so-called prearticular is a third coronoid.

HOLMGREN—STENSIÖ mention two small tooth-bearing bones in *Polypterus*, situated in the angle of the mandible and suggest: "Diese Knochen sind wohl als Koronoidea zu bezeichnen."

The mandible of *Polypterus* thus consists of two chondral ossifications, the mento-mandibular and the articular and five dermal bones, on the outside the dental-splenial and the angular-splenial, on the inside of a series of three coronoids (the most caudal being called the prearticular).

The preopercular sensory canal in *Polypterus* lodges only three neuromasts. The state of development of the preopercular canal in young larvae is described on p. 413 in this paper.

In a 24 mm specimen the dorsal portion of the *preopercular* bone is developed (fig. 16). It may be said to consist in its turn of two portions, one dorsal and one ventral. Yet, the author wants to make clear that there is nothing that indicates that these two parts have formed independently of each other. The ventral portion is a typical canal bone enclosing the preopercular neuromasts Nos. 2 and 3 (in the preoperculo-mandibular line Nos. 7 and 8). It has the shape of a rather flattened bone tube surrounding the canal. The dorsal end of the bone is developed into a lamella which forms the anterior portion of the preoperculum. It projects in a rostro-ventral direction as far as the level of the posterior portion of the eye. The proximal part of the lamella is comparatively thin and broad, but rostrally it tapers and grows more solid at the same time. There is nothing that indicates that it is anything but a process from the preopercular, at least not at the 24 mm stage and onward. The narrow ventro-rostral projection broadens in later stages and changes successively into the broad, solid cheek-plate so typical of *Polypterus*.

There is still another preopercular element in the 24 mm *Polypterus*. As said above (p. 413) the mandibular canal in connection with the first (ventral) neuromast of the three preopercular sense organs has not yet formed. This ventral sense organ is still situated in the surface of the skin and there is no

VOL. 28 1947

sign of invagination of the canal beginning. The neuromast only differs because of its size from a pit line organ. Yet, bone has begun to form in connection with this organ. It is a small, irregular disc of osseous substance, still very thin and formed in several small pieces. Because of its small size, the irregular shape and the position longitudinal to the sectioning direction, it is very difficult to represent the exact shape in a figure. It seems, however, from the blastematic primordium as if the blastema at least is divided into one rostral lump of cells and one caudal (fig. 16). This indicates a binary arrangement of the primordium as in *Amia*. In the next stage, the 27 mm specimen, the bone primordium has formed a tube, still independent, but in the 29 mm stage it is attached to the rest of the preopercular.

If there is a binary arrangement of the blastema of the ventral preopercular primordium a similar mode of development of the dorsal elements of the preopercular, as well, is probable. Further the binary origin of the suprascapular blastema (p. 442) seems to indicate that this may be the case even in other parts of the sensory canal system, except in the infraorbital line, where there are no binary primordia in Amia either. On the other hand there is no binary origin of the first nasal to be found (p. 426) in *Polypterus*.

From the development of the ventral portion of the preopercular, as well as from the observations on the canal elements of the maxillary, the premaxillary, the splenials and other canal bones, it seems probable that the development of the preopercular in *Polypterus* takes place in the following way.

The oldest portion of the preopercular is formed in connection with the dorsal neuromast. Bone has been formed there in the same way as is seen concerning the ventral neuromast in the 24 mm specimen. This dorsal canal bone sends out a process in a rostral direction. The bone in connection with the middle neuromast is also formed comparatively early, yet, later than the dorsal portion. This dorsal portion fuses gradually with the middle portion and in the meantime its rostral process continues growing rostro-ventrad. At the 24 mm stage the bone described above is formed and the rostro-ventral process has had the opportunity of reaching the furthermost point it will reach in the adult.

Larval stages of *Polypterus* have added no material to the theory of an independently formed "squamosal" element.

The same opinion is also maintained by HOLMGREN—STENSIÖ (1936) where a short summary of the various opinions concerning the supposed homologies of the preopercular is to be read (p. 395—396). Recently JARVIK (1947) has adopted the "squamosal" theory but has added no new arguments to the discussion.

From the exposition above, founded on the examination of ontogenetical evidence it does not seem possible in the author's opinion to maintain the theory of a closer relationship between the Crossopterygians and *Polypterus*.

VOL
28
194

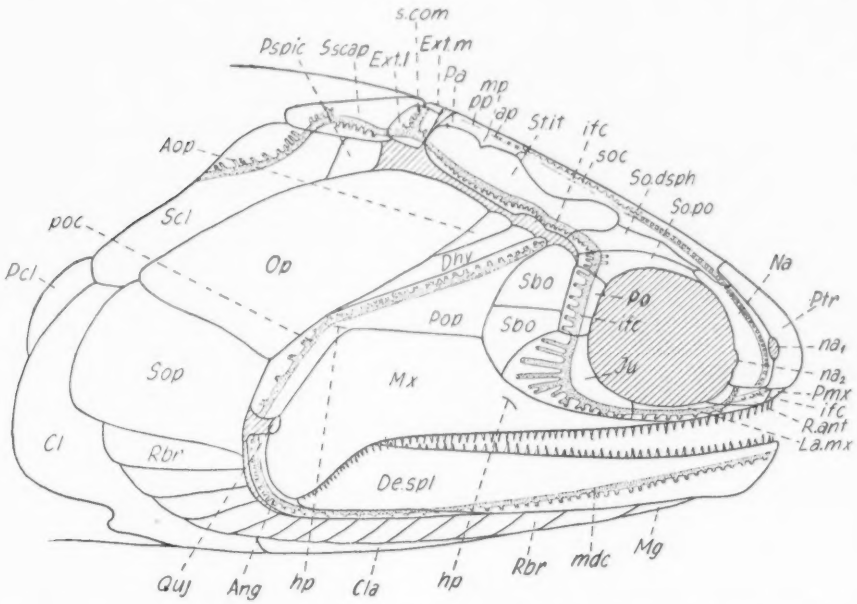

Fig. 27. *Glaucolepis stensiöi,* Trias (from NIELSEN 1942). *Ang* angular; *Aop* antoperculum; *Cl* cleithrum; *Cla* clavicle; *De.spl* dentalo-splenial; *Dhy* dermohyal; *Ext.l* lateral extrascapular; *Ext.m* medial extrascapular; *Ju* jugal; *La.mx* lacrimo-maxillary; *Mg* median gular plate; *Pcl* postcleithral; *Po* postorbital; *P.spic* postspiracular bone; *Ptr* postrostral; *Quj* quadratojugal; *R.ant* rostro-antorbital; *Rbr* branchiostegal ray; *Sbo* suborbital; *Scl* supracleithral; *So.dsph* supraorbito-dermosphenotic; *So.po* supraorbito-postorbital; *Sop* suboperculum; *Sscap* suprascapular; *ap* anterior pit-line; *hp* horizontal pit-line of the cheek; *ifc* infraorbital canal; *mdc* mandibular canal; *mp* middle pit-line; na_1, na_2 anterior and posterior nostrils; *poc* preopercular canal; *pp* posterior pit-line; *s.com* supratemporal commissure; *soc* supraorbital canal. Other letters as in fig. 21.

The evidence from the study of the development of other dermal bones than the "maxillary" points in the same direction.

If any connections with fossil fishes are going to be established the Palaeoniscids, as pointed out earlier in this paper, offer more profitable material for comparisons. Of special interest are the Palaeoniscids sensu strictu where a long maxillary is combined with a long preopercular as for instance in *Cheirolepis, Palaeoniscus* and other chiefly Palaeozoic types (cf. also fig. 27). In these forms a comparatively long cheek region is covered by the two bones together as in the case in *Polypterus.* The long rostral process of the preopercular may partly correspond to the rostral portion of the long preopercular in the Palaeoniscids mentioned, partly be an anterior process from this bone. The anterior portion of the preopercular in the Palaeoniscids would then be homologue of the proximal portion of the preopercular process in *Polypterus,* in the same way as the dorsal process from the second antorbital in *Polypterus* may be the homologue of the same process in *Amia, Sinamia* and *Lepidosteus,* that

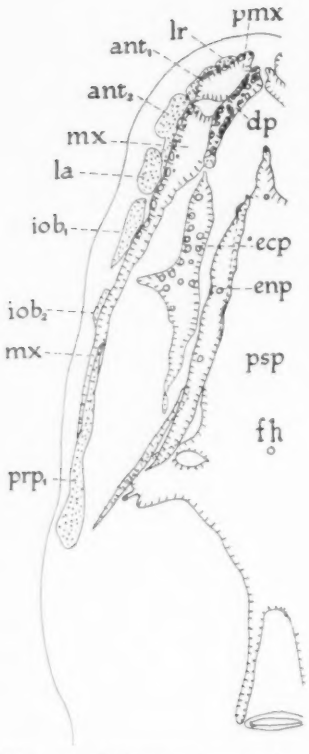

Fig. 28. *Polypterus senegalus*, 24 mm. Dermal bones of the skull in ventral view (24×1). Dotted areas, canal bones. Small circles, teeth.

is to say, after the loss of the sensory canal (cf. p. 424). The same argumentation also applies to the supracleithral in *Polypterus* (p. 443). As morphological evidence concerning *Polypterus* generally seems rather to point to a closer relationship between Palaeoniscids and Holosteans and this fish than along Crossopterygian lines, this attempt at interpreting the conditions in the cheek of *Polypterus* seems more advantageous. The same reason also applies to the attempt at homologising the caudal portion of the maxillary with a supramaxillary.

The existence in the *Polypterus* larvae of a separate ventral preopercular primordium recalls the conditions in *Brachydegmus* (DUNKLE 1939) from the lower Permian of Texas. In this fish the preopercular lacks the rostral cheek-plate, but, on the other hand, there is a separate small ventral preopercular, highly suggestive of the conditions in the 24 mm *Polypterus*.

The *vomer* in the 24 mm specimen is an extremely small ossification in the dense connective tissue between the anterior ends of the dermopalatines. It is even too small to act as a basis for teeth. Not until the 32 mm stage, has the vomer attained the size of a toothbearing bone. It carries two medial teeth. At later stages one more medial tooth develops and also lateral teeth appear. In the oldest specimen, a 125 mm *Polypterus bichir*, there are three medial teeth with a row of three lateral teth on each side.

The vomer is described by HOLMGREN—STENSIÖ (1936, p. 397). It is a very insignificant bone even in the adult and has been overlooked earlier. According to HOLMGREN—STENSIÖ the primordium is binary in the 30 mm stage. In *Polypterus senegalus* that is not the case, however.

The remaining dermal bones in the roof of the mouth, the *dermopalatine*, the *ecto-* and *entopterygoid* are already developed in the 24 mm specimen (fig. 28). The dermopalatine is well supplied with teeth along the whole ventral surface, as is also the anterior end of the ectopterygoid. The entopterygoid seems to have formed later and carries only a few teeth.

The *metapterygoid* (fig. 28) is, according to HOLMGREN—STENSIÖ, an ossification in the palato-quadrate. This does not appear to be the case. It arises as a typical dermal bone and covers, in the 24 mm stage, the entire medial

surface of the palato-quadrate. NIELSEN (1942) describes the same bone in *Glaucolepis* as a dermometapterygoid. It is found, as well, in various other Palaeoniscids (*Watsonichthys, Saurichthys, Birgeria, Elonichthys, Nematoptychius, Gonatodus*) and, as expressed by NIELSEN, the presence of an independent dermometapterygoid is a character common to many early Ganoids and, thus, a primitive character in *Polypterus*.

The *parasphenoid* in the 24 mm specimen (fig. 28) has largely acquired its definite shape (cf. HOLMGREN—STENSIÖ 1936). Only a few teeth are developed so far. The most anterior tooth is situated on the anterior tip of the bone, and there is no trace of the tooth-bearing "pad" mentioned by ALLIS (1922). This "pad" begins to form in the 27 mm specimen in this way. A system of lamellae develops from the dorsal surface of the originally formed bone lamella, some distance caudad. The new lamellae spread laterad and eventually form the definite lateral margin of the growing parasphenoid in this portion while the original, tooth-bearing part of the bone remains raised over the ventral surface.

According to ALLIS, who only had the opportunity of studying adult specimens, the "pad" has developed in relation to the teeth it bears—which is correct — and the dermal bone so formed has fused with an underlying bone "of distinctly different, membrane origin"—a surmise which is not correct as the "underlying bone" is formed as lamelliform processes from the tooth-bearing part.

VOL. 28 1947

SUMMARY.

The development of the chondral ossifications in *Polypterus* is described. During the ontogeny a small prootic is traced at early stages.

The supra- and infra-pharyngobranchials develop as in *Amia* and *Lepidosteus*.

The hyomandibular and accessory hyomandibular resemble these bones in Palaeoniscids.

The pattern of the sensory canal system in the snout of *Polypterus* is developed in principle as in the Holosteans.

An attempt is made to interpret the pattern of the sensory canal system in *Palaeonisciformes*.

The canal bones form as bone-tubes from which flanges develop mesiad and laterad, the bone, thus, gradually changing into a flat bone pierced by a canal. The age of the material has not allowed the study of the blastematic primordia, except in the suprascapular where binary primordia form.

The frontal develops as three separate elements which fuse.

The rostral in *Polypterus* is homologous with the medial portion of the rostral in *Amia*.

The row of infraorbital canal bones posterior to the rostral comprises a lateral rostral, homologous with the lateral portions of the rostral in *Amia,* two antorbitals, together homologous with the single antorbital in *Amia,* a lacrimal, two infra- (sub-) orbitals and a postorbital.

A normal tooth-bearing premaxillary develops, but, during the ontogeny it fuses with three infraorbital bones, the lateral rostral and the two antorbitals to form a compound premaxillary-infraorbital.

The maxillary develops as a normal, tooth-bearing maxillary. In early stages it consists of an anterior flat, triangular tooth-bearing portion and a long, narrow, caudal process, the posterior part of which joins a similar rod-like rostral process from the preopercular without fusing with it. The maxillary fuses with the two infra- (sub-) orbitals to form a compound maxillary-infraorbital. The rod-like caudal process of the maxillary is possibly the homologue of a supramaxillary.

The anterior of the two "quadrato-jugals may be the homologue of the postero-ventral portion of the Palaeoniscid maxillary and the posterior to the quadrato-jugal found in some Palaeoniscids.

A separate dermosphenotic develops, but, fuses early with the auto-sphenotic.

Separate intertemporals and supratemporals develop, but, fuse to form the supratemporo-intertemporal which covers the space occupied during the early ontogeny by a transitory parietal primordium.

The parietal is missing in the adult *Polypterus,* and develops as an insignificant primordium which never forms definite bone, the space covered by the parietal primordium being overgrown by the medial edge of the supratemporo-intertemporal.

The dentary-splenial is a compound bone formed by the dentary sensu strictu and three tube-like splenials, of which the first is still free in a 24 mm specimen.

An angular-splenial is formed in the same way by an angular and two splenials.

Three coronoid bones develop on the medial side of the mandible. The third and largest coronoid is the so-called prearticular.

In a 24 mm specimen, the preopercular still consists of two pieces. One is a large dorsal portion formed in connection with two neuromasts. It is a broad well-developed bone and has the rostral process, typical of *Polypterus,* which stretches across the cheek together with the caudal maxillary process. The ventral portion of the preopercular is just beginning to form in the youngest specimen examined. The preoperculum and the maxillary in *Polypterus* are compared with the same bones in Palaeoniscids.

The development of the vomer and the metapterygoid is described. The latter bone is a dermal ossification as in Palaeoniscids.

As to the phylogenetic position of *Polypterus,* the author entirely agrees with ROMER (1946): "*Polypterus* is a good Actinopterygian, and a primitive one."

VOL
28
194

It shows relationship, as far as the skull is concerned, with Palaeoniscids as well as with Holosteans, but, is not more related to the Crossopterygians than the other primitive Actinopterygians.

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VOL
28
194

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VOL. 28 1947

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KEY TO TEXT-FIGURES.

ac auditory capsule.
ah accessory hymandibular.
aml anterior mandibular line.
an anterior nostril.
ang angular, sensu strictu.
ant antorbital.
ant_1 first antorbital bone.
ant_2 second antorbital bone.
apl anterior head line of pits.
art articular.
b brain.
bb basibranchial.
cb_1—cb_2 ceratobranchials.
ch notochord.
chy ceratohyal.
dc dentary, sensu strictu.
dp dermopalatine.
dso dermosphenotic neuromast.
dspc dermosphenotic.
ecp ectopterygoid.
ect ectethmoid.
enp entopterygoid.

epc epiphyseal cartilage.
epi epibranchial.
esc$_1$ lateral extrascapular.
esc$_2$ medial extrascapular.
fh foramen hypophyseos.
fpo foramen for nn profundus et oculomotorius.
fr frontal.
fr$_1$ first frontal.
fr$_{2+3}$ second and third frontal fused.
gg glossopharyngeal ganglion.
gpl gular pit line.
gs gill slit.
hm hyomandibular.
hmpl horizontal mandibular pit-line.
hpl$_1$ anterior portion of horizontal cheek line of pits.
hpl$_2$ posterior portion of horizontal cheek line of pits.
io$_1$—*io*$_8$ infraorbital neuromast 1—8.
iob$_1$ first infraorbital bone.
iob$_2$ second infraorbital bone.
ioc infraorbital sensory canal.
iph infra-pharyngobranchial.
it intertemporal.
ito intertemporal sense organ.
la lacrimal.
lc labial cartilage.
lr lateral rostral.
mo$_1$—*mo*$_5$ mandibular neuromasts 1—5.
mpl middle head line of pits.
mplo sense organ in middle head line of pits.
mx maxillary, sensu strictu.
n nerve.
na nasal.
na$_1$ first nasal ("os terminale").
na$_2$ second nasal ("accessory nasal').
na$_3$ third nasal.
npl nasal line of pits.
nplo sense organ in nasal line of pits.
oc occipital ossification.
op opisthotic.
pa parietal.
pml primary mandibular line of pits.
pmx premaxillary, sensu strictu.
pn posterior nostril.
po postorbital.
po$_1$—*po*$_3$ preopercular neuromasts 1—3.
ppl posterior head line of pits.
pra prearticular.
pro prootic rudiment.
prp$_1$ dorsal portion of preopercular.
prp$_2$ ventral portion of preopercular.
psp prasphenoid.
pt "posttemporal".
q quadrate.
qj quadrato-jugal.
rc rostral commissure.
ro rostral.
sco supratemporal commissure neuromasts.
so supraorbital sensory canal.
so$_1$—*so*$_6$ supraorbital neuromasts 1—6.
sp$_1$—*sp*$_5$ splenials 1—5.
spc sphenotic.
spd sphenoid.
spi spiracle.
ssco suprascapular neuromast.
st supratemporal.
sto supratemporal sense organ.
su-it supratemporo-intertemporal.
suph suprapharyngobranchial.
vg vagus ganglion.
vmpl vertical mandibular line of pits.
vpl vertical line of pits.

VOL. 28 1947